Life History of the Caligid Copepod *Lepeophtheirus dissimulatus* Wilson, 1905 (Crustacea: Caligoida)[1]

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Copepods of the family Caligidae are found as external parasites on both fresh and salt water fishes throughout the world. Even with their wide distribution, relatively little is known about their life history. The presentation of the life history of *Lepeophtheirus dissimulatus,* a caligid found on salt water fishes, should provide more information on the life history and general biology of this group of copepods.

Although there are many references to immature and juvenile or larval stages (reviewed by Heegaard, 1947: 21–31), only a few workers have had the material to describe the complete life history of a caligid. Through methods described below, the author was able to obtain a series of Hawaiian specimens representing all of the stages of development of *L. dissimulatus.*

Lepeophtheirus dissimulatus is one of the more common parasitic copepods of Hawaiian acanthurid (surgeon) fishes. The species is not limited only to Hawaiian fishes but is known from a wide variety of localities and a wide variety of hosts (Lewis, in press). Even with its wide distribution, in both the Atlantic and Pacific oceans, larval stages have been described only once, by Shiino (1959:309), from fishes of the Revilla Gigedo Islands.

Attempts to rear the copepod from the egg to the adult in culture were only partially successful. Ovigerous adult females were placed in clean finger bowls partially filled with cotton-filtered or unfiltered sea water. Circulation of the water was accomplished by means of a fine jet of air from a slender glass tube immersed in the medium. The water was changed at least once every 8 hr and usually more frequently. At the time the eggs, carried by the female, hatched, a portion of the first nauplii, the first larval stage, was removed with a wide-mouthed pipette and placed in small stender dishes. The remaining nauplii were left in the finger bowl and the adult female was removed and placed in a separate bowl. Water in the finger bowls was circulated in the same manner as above and changed at the same time intervals. Water in the stender dishes was not circulated but instead was changed at more frequent intervals, every 3–4 hr. As moulting occurred into the second naupliar stage, the newly moulted second nauplii were transferred to new finger bowls or stender dishes except for three to four individuals which were preserved in either 10% buffered formalin or 95% ethyl alcohol. Shortly after the second naupliar stage moulted into the succeeding stage, the copepodite, a piece of loosely woven nylon cloth was placed in the dishes to offer a substrate for attachment. (It was found that the copepodite stage is the stage which attaches to the host.) In addition, pieces of host tissue were placed in some of the dishes. The host tissue was left in the dishes for 1 hr and then removed and the animals transferred to a new dish in order to reduce contamination and bacterial action.

The mortality rate between the first and second naupliar stages was high and appeared to be partially due to the inability of the nauplius to break out of the old cuticle. The rate from the second naupliar stage to the copepodite was relatively low. Out of the 30 attempts that were made to rear the copepod, each with at least one female carrying from 20–60 eggs, one copepodite was obtained that attached to the nylon cloth placed in the dish. The remaining copepodites died without attaching and the single copepodite that attached died immediately thereafter. None of the copepodites attached to the host tissue placed in the dishes.

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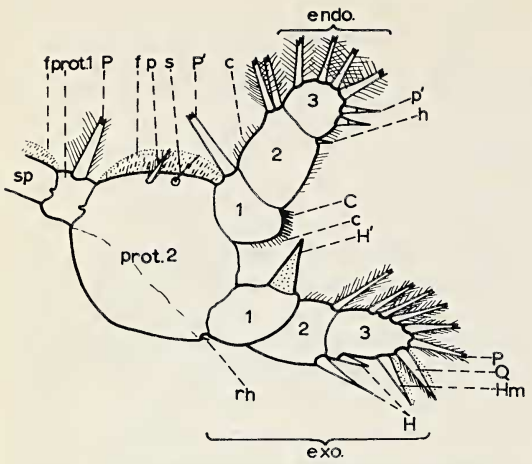

FIG. 1. Hypothetical thoracic leg of *Lepeophtheirus dissimulatus,* showing the various armament components. *C,* Heavy setae; *c,* fine setae; *endo,* endopodite; *exo,* exopodite; *f,* membrane; *H,* well-developed spine; *H',* laterally projecting spine appearing as a continuation of segment; *h,* poorly developed spine; *Hm,* membrane margined spine; *P,* large plumose setae; *P',* large naked setae; *p,* small plumose setae; *p',* small naked seta; *prot,* protopodite; *Q,* seta (or spine) plumose on one side and membrane-margined on other; *rh,* spinule; *s,* hairlike seta; *sp,* sternal plate.

Because of the failure of the culture material and in order to obtain a complete timed series of developmental stages, attached copepodites were taken from host material and placed in individual stender dishes. After these copepodites moulted into the first chalimus (the following stage), the time was noted until the succeeding moult, into the second chalimus. To ascertain the time passed in each stage after the first chalimus, specimens of the previous stage were taken from the host and treated as above. Due to the mortality rate under laboratory conditions, many specimens of each stage had to be collected so that one would pass through the succeeding stage. Because of the inability to get any number of specimens to pass through each stage and due to the necessity of submitting the larvae to laboratory conditions, the time indicated for each stage in Figures 2–7 should be regarded as indicative, not conclusive.

The descriptions of the body, appendages, and processes of all of the developmental stages and the adult is followed by a discussion of the general behavior of the various developmental stages. The graphical figures included in the text (Figs. 2–7) give the means and ranges of various measurements of the larval forms.

Larval specimens other than nauplii were killed and preserved in 95% ethyl alcohol. Specimens to be dissected were placed in 85% lactic acid to soften and clear them, stained with methyl blue dissolved in 85% lactic acid, and dissected in clear 85% lactic acid.

Drawings of the total animal were made from specimens placed in 85% lactic acid and covered with a 9 mm cover slip. The cover slip was raised slightly above the younger specimens by thin pieces of glass so that the specimen was not distended. A camera lucida and a Bausch and Lomb arc projector were used to make the drawings of the total animal. Drawings of the appendages and processes were made, with the use of a camera lucida, from appendages and processes either in situ on the whole mount or dissected off and mounted in Hoyer's mounting medium. Measurements were made with an ocular micrometer.

The terminology used, with some exceptions which are given in the text, is that used in Lewis (in press). To facilitate the use of the thoracic leg tables, a hypothetical thoracic leg is shown in Figure 1, giving all of the component parts of the armament of the thoracic legs discussed in tabular form in this publication. Further, a table of the hypothetical thoractic leg is given below in Table 1.

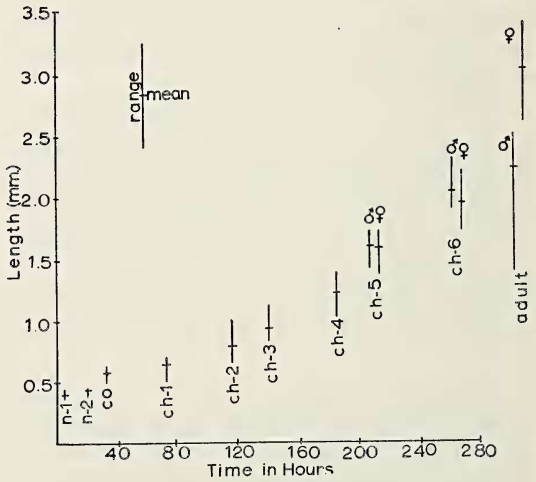

FIG. 2. Greatest length of body, excluding setae, in developmental stages of *L. dissimulatus. n,* Nauplius; *co,* copepodite; *ch,* chalimus.

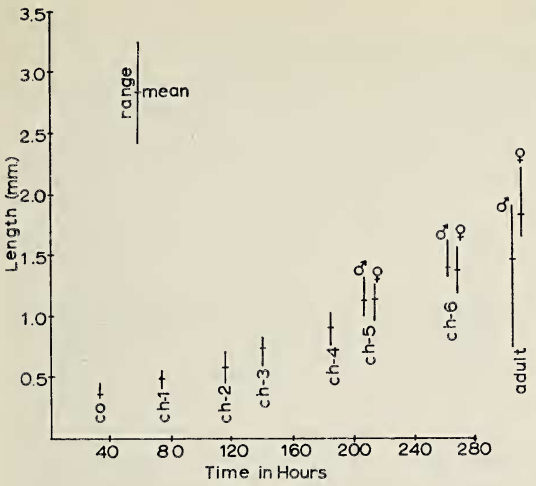

FIG. 3. Greatest length of cephalothorax, including frontal plates, of developmental stages of *L. dissimulatus*. *co,* Copepodite; *ch,* chalimus.

DEVELOPMENT AND DESCRIPTION OF LIFE HISTORY STAGES

As the eggs are extruded out of the oviducal opening at the posterior end of the genital segment they are fertilized by sperm from the seminal receptacle (Wilson, 1905:526). Two spermatophores are implanted by the male on the external posterior ventral surface of the female genital segment and open into the two oviducts through the seminal receptacles (Wilson, 1905:527). The disk-shaped fertilized eggs are extruded as a uniseriate chain (Fig. 8*a*). Each egg is wrapped in a cuticular material, presumably secreted by a cement gland in the genital segment of the female, that remains attached to the female until after the eggs hatch (Fig. 8*b*). The covering appears to serve as a protective structure for the eggs and developing embryos and as a means of connecting the eggs together in a string.

Because of the flattening of the fertilized eggs, development is difficult to observe. From 13–20 hr (at room temperature, approximately 23 C) after extrusion, a reddish-colored eye spot becomes visible on the yellowish or whitish embryo. From 30 to 40 hr (at room temperature) after extrusion, movement is visible within the egg. As the movement of the embryo increases, the egg expands and finally ruptures. Hatching occurs regularly, the distal egg hatching first, the proximal last. A lapse of between 2 and 10 min occurs between the hatching of one egg and the hatching of the succeeding one. In almost all cases, the egg chamber ruptures on the inner side of the egg string (i.e., the surface nearest the median longitudinal axis of the female). The first nauplius, by sporadic violent movements of its appendages, works its way out of the egg case and, after a short period of rest in which some swelling occurs, assumes the characteristic jerky, free-swimming habit of the naupliar stages.

Body

The externally unsegmented body of the first nauplius (Fig. 8*c*) is of a general obovoid shape in both dorsal and lateral aspects. The greatest length is slightly more than twice the greatest width, and the anterior end is broadly curved. The lateral margins of the posterior one-half of the body curve inward regularly to the irregularly-margined posterior end. The posterior end of the body has a slight median projection and two indentations, one on each side, from which the balancers arise. The balancers (Fig. 16*k*) are unsegmented, slightly curved, rodlike structures that project laterally and have their distal end slightly flattened.

The cuticle of the first nauplius is, in most specimens, slightly larger than the inner body;

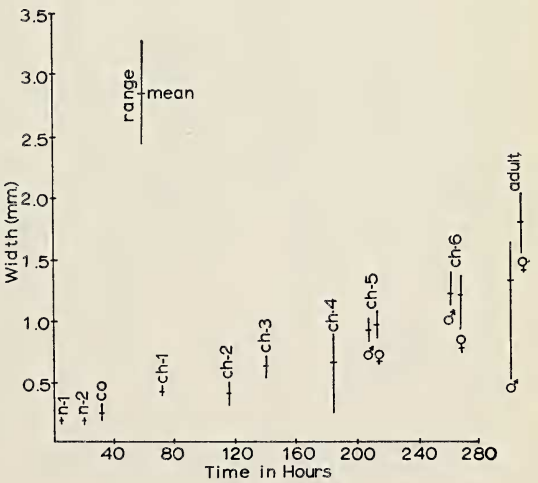

FIG. 4. Greatest width of body, excluding marginal flanges, of developmental stages of *L. dissimulatus*. *n,* Nauplius; *co,* copepodite; *ch,* chalimus.

TABLE 1

ARMATURE OF HYPOTHETICAL THORACIC LEG SHOWN IN FIGURE 1

MARGIN	STERNAL PLATE	PROTOPODITE 1	PROTOPODITE 2	EXOPODITE 1	EXOPODITE 2	EXOPODITE 3	ENDOPODITE 1	ENDOPODITE 2	ENDOPODITE 3
Outer	f		1rh		1H	2H,1Hm,1Q	c,C	c,1h	c,2p',2P
Inner		1P	f,1p,1s	1H'	c,1P	c,5P	1P'	c,2P	2P

a distinct space is visible between the anterior end of the body and the cuticle. There is indistinct evidence of internal segmentation posteriorly. The general body color in life is light yellow with numerous red and blue pigment spots scattered over the surface. The eyes are visible as two minute, clear, round lenses, one on each side of an irregular, reddish-pigmented region in the anterior portion of the body. The alimentary tract is not visible, neither are the mouth nor the anus. Large globules of material, presumably yolk, are evident, clustered in an indistinctly delimited, oblong mass extending posteriorly from just behind the ocular region.

The first nauplius possesses three sets of appendages (described later), the uniramous antennules, biramous second antennae, and biramous mandibles in this order proceeding posteriorly. All of these appendages possess long, lightly plumose setae that presumably function as flotation mechanisms and in swimming.

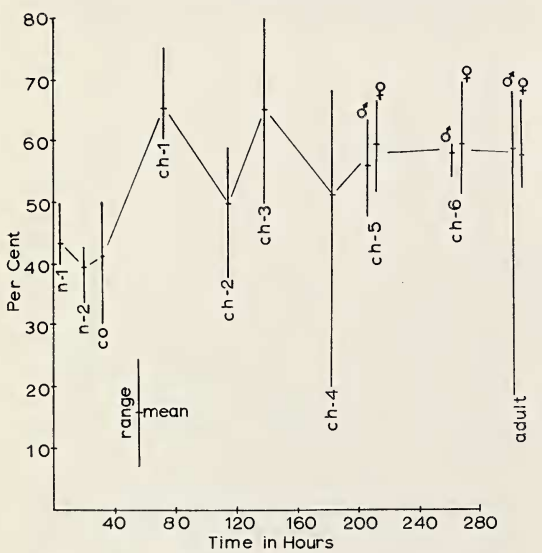

FIG. 5. Greatest width as a per cent of total body length, excluding setae, of developmental stages of *L. dissimulatus*. *n*, Nauplius; *co*, copepodite; *ch*, chalimus.

The first naupliar stage lasts for 4½–13 hr with an average of 6½ hr (based on nine hatchings at room temperature, approximately 23 C). After this time the movement of the animal decreases slightly and the cuticle splits longitudinally at the dorsal anterior end. The nauplius then wriggles violently and breaks through the split, freeing itself from the cuticle.

The body of the second nauplius (Fig. 8*d*, *e*) is similar to that of the first, although the length from the mandibles to the posterior end of the body is greater. The greatest length, excluding the appendages, is almost 2½ times the greatest width. The body is very slightly flattened dorsoventrally in cross section, the anterior end is broadly curved, and the lateral margins are flatly convex. The posterior end of the body is similar to that of the first nauplius although the balancers are slightly larger and arise from two small, circular, platelike processes in the posterior lateral indentations (Fig. 16*l*).

The bodies of older second nauplii have a small space between the anterior end and the cuticle. There is distinct evidence of internal segmentation, similar to the segmentation of the copepodite, visible inside the cuticle of older specimens but not visible on the external surface. The alimentary tract is indistinct and incomplete, visible only as a cluster of yolk globules along the median longitudinal axis just posterior to the ocular region.

The basic structure of the three sets of appendages of the second nauplius is similar to that of the first. The armature, however, is slightly different. This stage lasts for 9½–19 hr with an average of 14½ hr (based on eight hatchings at room temperature, approximately 23 C). Just prior to moulting into the copepodite stage, the movement of the animal be-

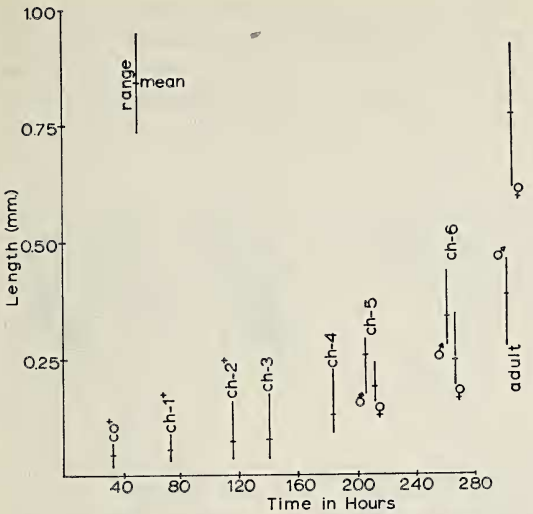

FIG. 6. Greatest length of genital segment of developmental stages of *L. dissimulatus. co,* Copepodite; *ch,* chalimus; +, measurement includes both genital segment and abdomen (one segment in early stages).

comes sporadic, stopping at times and then becoming vigorous. During one of the vigorous periods of movement a crack appears in the anterior dorsal portion of the cuticle and the copepodite wriggles out in the same manner as in the previous moult.

The change from the second nauplius to the copepodite is the greatest change that occurs in a single moult during development. In one moult the body is divided from an externally unsegmented structure into a cephalothorax consisting of the head, maxilliped-bearing segment, and first pedigerous segment. Further, four free segments are visible posterior to the cephalothorax. The first of these segments bears the second thoracic legs, the second bears a pair of posteriorly directed spines that may be the predecessors of the third thoracic legs, the third free segment is naked but will later give rise to the fourth thoracic legs, and the fourth free segment, to which the caudal rami are attached, will later differentiate into the genital segment and abdomen.

Not only does the body break up from a relatively undifferentiated second nauplius to a copepodite with a composition comparable to that of the adult, but also most of the appendages and processes are now present. Besides the antennules, second antennae, and mandibles that were present on the first and second nauplius, the postoral processes, maxillae, maxillipeds, and first two pairs of thoracic legs have been added and the caudal rami are now present.

The general shape of the copepodite body (Fig. 8*f*) is ovoid in both dorsal and lateral aspects. The greatest width, that of the cephalothorax, is less than one-half the greatest length (Fig. 5). The anterior cephalothoracic margin is sharply convex and the lateral margins are flatly convex. A pair of V-shaped indentations, or sinuses, are visible in the posterior lateral margin of the cephalothorax. These posterior sinuses are found at the junction of the posterior surfaces of the median and lateral cephalothoracic areas and suggest that the lateral areas are distinct from the median and are an outgrowth of the cephalon. This is further indicated by the longitudinal cephalothoracic grooves which, in the copepodite, run anteriorly for a very short distance from the apex of the posterior sinuses. The median cephalothoracic area does not extend past the posterior lateral area and its posterior margin is irregular. The eyes are distinct and similar to those of the naupliar stages.

The free second pedigerous segment is wider than long, its greatest width being 1.3 times the length. Both the anterior and posterior margins

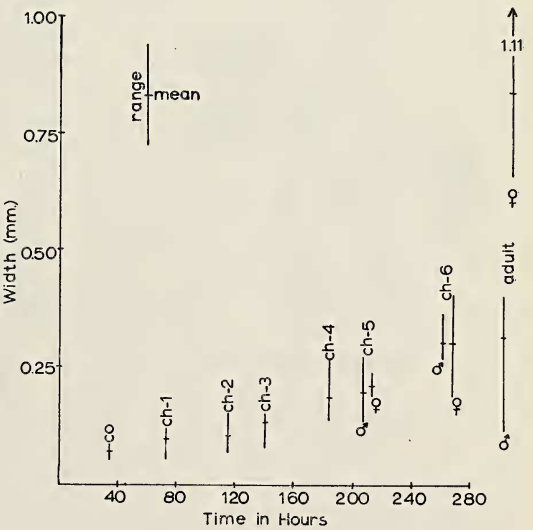

FIG. 7. Greatest width of genital segment of developmental stages of *L. dissimulatus. co,* Copepodite; *ch,* chalimus.

are distinct, the anterior being irregularly convex and the posterior irregularly concave; the lateral margins are broadly convex. The free third pedigerous segment is approximately two-thirds the width of the second and is slightly wider than long. The lateral margins of the segment are broadly convex in younger specimens, straight in older; the width of the posterior end of the segment is slightly greater than that of the anterior in older specimens but equal to or

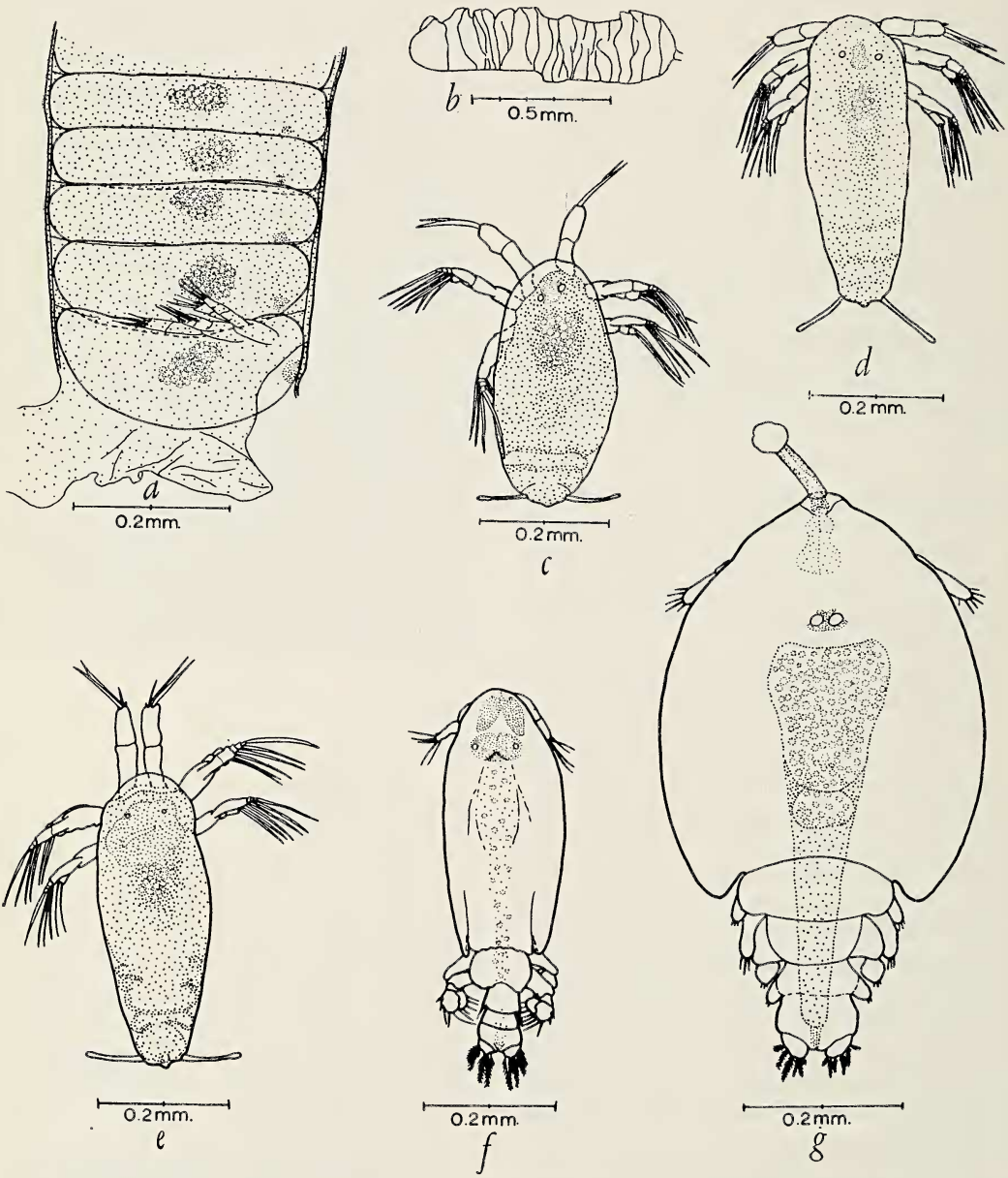

FIG. 8. Egg string of *L. dissimulatus* and body of developmental stages from nauplius to first chalimus. *a*, Posterior end of ruptured egg string, showing first nauplius just emerging; *b*, empty egg string after hatching; *c*, dorsal view of first nauplius; *d*, dorsal view of early second nauplius; *e*, dorsal view of late second nauplius; *f*, dorsal view of copepodite; *g*, dorsal view of first chalimus. Stippled circles, yolk material.

slightly less than the width of the anterior end in younger specimens. The third pedigerous segment bears a single naked, spinelike process projecting from each of the posterior lateral corners (Fig. 12*a*). The relationship of this process to the future third thoracic leg is unknown although Heegaard (1947:63, fig. 8) figures a pair of lobate appendages in the same region as the spines and indicates that they become the third thoracic legs of *Caligus curtus*. The free fourth pedigerous segment is short, its greatest width being almost 3 times its length. The anterior margin is concave, the posterior convex. There is no indication of the fourth thoracic legs.

The free fourth segment, the future genital segment and abdomen, is slightly shorter than the combined lengths of the third and fourth pedigerous segments, and the width is slightly greater than the length. The lateral margins are flatly convex, and the lateral posterior margins are concave, forming the attachment surface, and possibly an articulation surface, for the caudal rami. The posterior medial margin of the segment is bilobed, and the anal region is evident as a minute, V-shaped depression between the lobes.

The copepodite possesses a spikelike rostrum on the anterior end of the cephalothorax (Fig. 13*a*). The frontal organ is now visible, although rather indistinctly, and is represented by two large ovoid bodies at the anterior end of the cephalothorax that are connected to the rostrum by a slender, tubelike process. The alimentary tract is visible as two convex lines extending from just behind the eyes posteriorly for approximately one-third the length of the cephalothorax. The tract is visible posterior to the two convex lines only as a slender mass of yolk globules along the median longitudinal axis and extending posteriorly to the free third pedigerous segment. There does not appear to be an oral opening.

The length of time spent in the copepodite stage is not known due to the inability of getting a copepodite to attach to a substrate and moult into the first chalimus in the laboratory. In order to determine the method of attachment, observations were made on specimens of copepodites attached to host material collected in the field. The copepodite attaches to the host by means of the second antennae, secretes a frontal filament, and then after a short period of time moults into the first chalimus. This process is described in detail in the portion of the paper devoted to the general behavior of the developmental stages. The only visible difference between the free-swimming and attached copepodites is the slightly larger frontal organ in the attached forms. All of the appendages and processes and the general body structure are identical. Heegaard (1947:53–65), however, describes two copepodite stages for *Caligus curtus*, the first copepodite moulting into the second shortly after the host is found. In addition he describes a "pupal stage" that is passed within the loosened but unshed second copepodite cuticle. Neither the second copepodite stage nor the pupal stage were found in *Lepeophtheirus dissimulatus*.

The change from the copepodite to the adult is gradual for the most part. There are exceptions to this in some of the appendages such as the first and second thoracic legs but, in general, the transition occurs in a step-by-step manner through the six chalimus stages which are found between the copepodite and the adult.

The first chalimus (Fig. 8*g*), attached to the host by the frontal filament, is dorsoventrally flattened. The body is ovoid in a dorsal view and the greatest length, including the frontal region but not the frontal filament, is approximately 1.2 times the greatest width. The cephalothorax consists of the cephalon, maxilliped-bearing segment, and first pedigerous segment as in the copepodite. The second, third, and fourth pedigerous segments, in addition to the single segment that will later form the genital segment and abdomen, are free. The anterior margin of the cephalothorax is broadly curved except for an irregular median swelling in the region of the frontal filament. The lateral cephalothoracic margins flare slightly anteriorly, just posterior to the antennule base, and then curve flatly posteriorly. The posterior sinuses are distinct but are formed of the anterior lateral margin of the second pedigerous segment and the inner margin of the posterior lateral cephalothoracic area, not the outer margin of the median cephalothoracic area and the inner margin of the posterior lateral cephalothoracic area as in the copepodite. The median margin of the thoracic area is flatly

convex and extends between the apices of the posterior sinuses. The eyes are similar to those of the preceding stages and are situated in the anterior one-third of the cephalothorax. Cephalothoracic grooves are indistinctly present or absent although some irregular dorsal grooves are usually present in the anterior part of the body.

The free second pedigerous segment is much wider than in the copepodite, being more than 3 times as wide as long. The lateral margins are smoothly convex, the posterior margin flatly convex. The free third pedigerous segment is approximately 2½ times wider than long, the posterior end is narrower than the anterior, the lateral margins are flatly convex, and the posterior margin is flat. The third thoracic legs are now present, the spinelike processes of the copepodite being absent. The fourth pedigerous segment is shorter than the third, the width is slightly more than twice the length, and the posterior region projects laterally slightly at the junction of the now present fourth thoracic legs. The posterior margin of the segment is indistinct and irregular.

The combined genital segment and abdomen (Fig. 12*b*), that form the fourth free segment, are similar in both shape and measurements to that of the copepodite.

The frontal region (Fig. 13*b*) is slightly irregular; the rostrum of the copepodite is absent. The frontal organ consists of two lobate processes at the base of the frontal filament, an additional two lobate processes attached to the posterior surface of the first two, and an irregular indistinct area posterior to the second set of processes. The frontal region is not distinctly separated from the cephalothorax although an indistinct groove is present on the ventral surface, extending from the lateral margin, in the region of the antennules, posteriorly and then across the ventral surface.

The first chalimus stage lasts for approximately 40 hr (based on two specimens kept at room temperature, approximately 23 C) at which time the specimens moult into the more elongate second chalimus.

The general shape of the second chalimus (Fig. 9*a*, *b*) is similar to that of the first chalimus. The cephalothorax now includes the second pedigerous segment in addition to the first. Late in this stage, however, the division between the cephalothorax and the third pedigerous segment becomes indistinct (Fig. 9*b*). The greatest length of the cephalothorax, including the frontal region, is approximately 1½ times the greatest width, considerably longer than the cephalothorax of the first chalimus. The increase in length is presumably due to the inclusion of the second pedigerous segment in the cephalothorax. The anterior margin of the cephalothorax is broadly rounded except for the median protrusion of the frontal filament; laterally, the margin turns posteriorly sharply, then flares slightly to the lateral cephalothoracic margins. The lateral margins are wavy in some specimens and smooth in others although the entire margin is generally convex. The posterior cephalothoracic margin is four-lobed in the early second chalimus, with two large lobes in the lateral region of each side. In older specimens of this stage, in which the division between the cephalothorax and the third pedigerous segment is indistinct, the inner two lobes are not visible and the median cephalothoracic area, the third pedigerous segment, projects well past the lateral areas. The posterior sinuses are distinct as two small, V-shaped depressions between the two lobes in the younger specimens and between the inner margin of the lateral areas and the outer margin of the median cephalothoracic area in the older specimens. Thus far then, the posterior sinuses appear to be due to the unequal growth of the lateral and medial regions of the cephalothorax. The dorsal cephalothoracic grooves are indistinct, consisting of a single, very short groove extending anteriorly from the apex of each of the two posterior sinuses.

The third pedigerous segment, free in the early second chalimus, tapers evenly from the junction with the second pedigerous segment to the junction with the free fourth pedigerous segment. The greatest length of the segment is approximately four-fifths the greatest width and about one-fifth that of the cephalothorax. The free fourth pedigerous segment flares outward from the junction of the third to the attachment of the fourth legs, at the posterior end of the segment. The greatest width of the segment is approximately 1.6 times the greatest length, slightly more than one-half that of the third pedigerous segment. The division between the

third and fourth pedigerous segments is distinct, between the fourth and the genital-abdominal segment also distinct although sometimes faint in younger specimens.

The combined genital segment and abdomen (Fig. 12*c*) is slightly shorter than the third pedigerous segment, and its greatest width is slightly more than its length. The lateral margins are flatly convex; the lateral posterior margins are flat or slightly concave and form the place of attachment for the caudal rami. The anal laminae are visible as two knoblike projec-

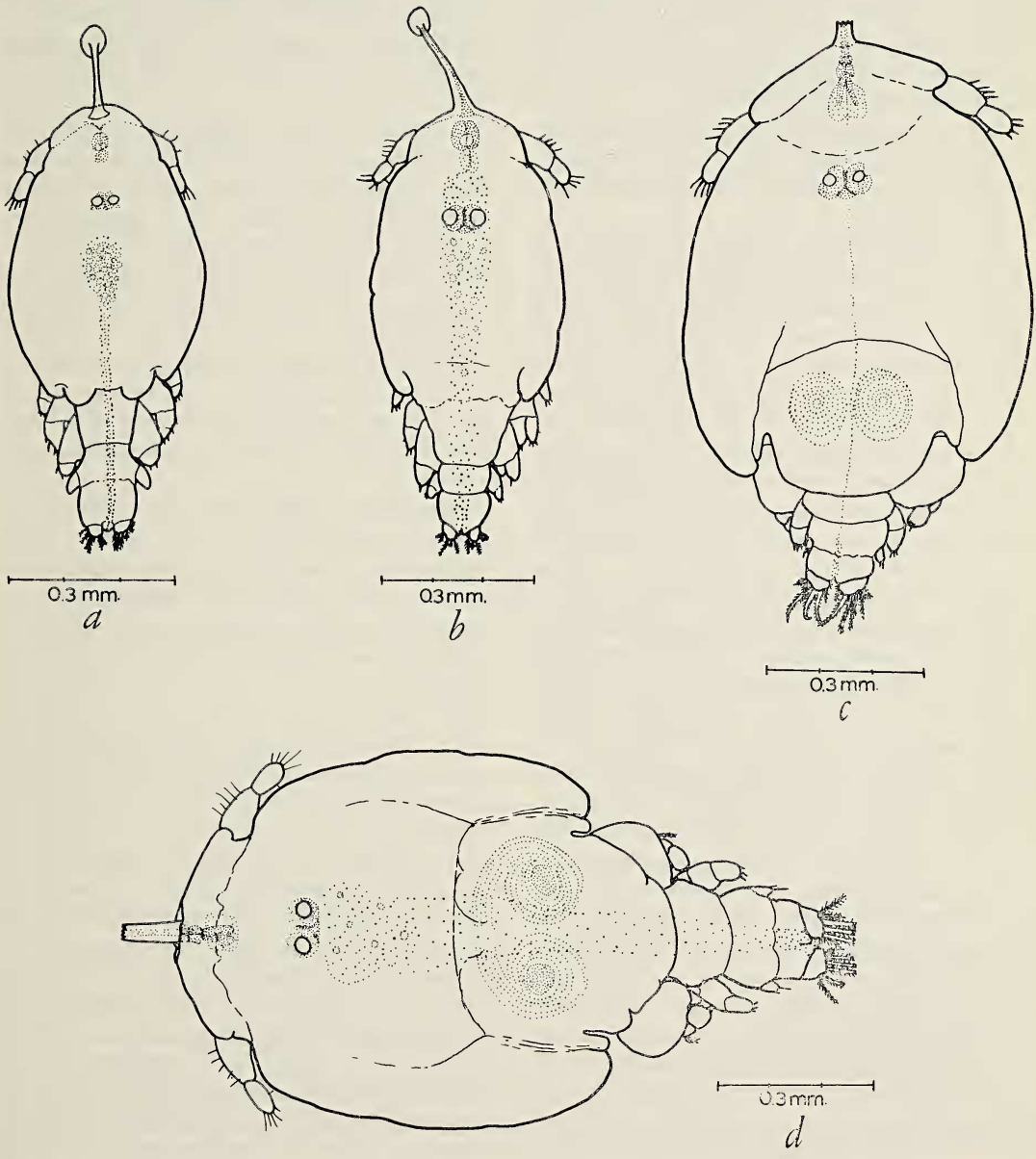

FIG. 9. Body of second, third, and fourth chalimus developmental stages of *L. dissimulatus*. *a*, Dorsal view of early second chalimus; *b*, dorsal view of late second chalimus; *c*, dorsal view of third chalimus; *d*, dorsal view of fourth chalimus. Stippled circles, yolk material.

tions and form the middle of the posterior surface of the segment.

The frontal organ of the second chalimus (Fig. 13*c*) is similar to that of the first chalimus although more distinct. The lobes at the proximal end of the frontal filament are contiguous along the median longitudinal axis of the body, forming a single ovoid structure; the lobes posterior to the first set are slightly smaller than in the preceding stage. The alimentary tract now appears complete although the anterior end is still filled with yolk granules.

The 10 specimens maintained successfully in the laboratory, at room temperature (approximately 23 C), remained in the second chalimus for about 42 hr.

The third chalimus (Fig. 9*c*) is somewhat wider than the second. The greatest length, including the frontal region but not the frontal filament, is approximately 1.3 times the greatest width. The cephalothorax now includes the first three pedigerous segments, the condition occurring in the adult. The fourth pedigerous segment is free and forms the connection between the cephalothorax and the now indistinctly differentiated genital segment and abdomen. The frontal region (Fig. 13*d*) is still indistinctly separated from the cephalothorax. The anterior margin of the frontal region is flatly tapered from the projection of the frontal filament laterally. The lateral portions of the frontal margin are evenly rounded and join the lateral margins of the cephalothorax at a slight indentation marking the origin of the groove incompletely dividing the frontal region from the cephalothorax. The lateral margins of the cephalothorax are smoothly convex, the posterior lateral corners rounded. The posterior sinuses are distinct and U-shaped; the lateral margins of the median thoracic area are continuous with the inner margins of the sinuses. The median thoracic area extends posteriorly past the posterior extensions of the lateral areas. The reddish-pigmented regions of the eyes encircle all but the outer portion of the lenses, a large increase in the amount of pigmented material over the preceding stages. The cephalothoracic grooves are distinct, the major ones forming an H. The longitudinal grooves of the H extend anteriorly and curve medially from their origin just lateral to the apices of the posterior sinuses. The two grooves are connected by an anteriorly curving cross groove in their anterior region. Other indistinct grooves are present in the anterior region of the cephalothorax.

The free fourth pedigerous segment is short and partially covered by the posterior portion of the median cephalothoracic area. The greatest length of the segment is approximately one-half the greatest width. The lateral margins are convex; the posterior margin is distinct, completely separating the segment from the genital segment.

The genital segment (Fig. 12*d*) is short, the length slightly more than one-half the greatest width, approximately equal to the length of the fourth pedigerous segment. The lateral margins are convex anteriorly and indented posteriorly. The posterior margin is light but distinct, and the abdomen is now considered distinct from the genital segment. A pair of one-segmented dactyliform processes, the fifth legs, are visible extending posteriorly from the posterior lateral surface of the genital segment. The distal end of the fifth leg is rounded and bears two plumose setules.

The abdomen (Fig. 12*d*) is short, the greatest length slightly less than that of the genital segment, the greatest width approximately 2½ times the length. The lateral margins are convex and the posterior margins curve medially to the bilobed anal region, composed of the anal laminae.

The frontal organ (Fig. 13*d*) is slightly smaller than that of the second chalimus and consists of four parts. The first part is formed of two oval bodies at the base of the frontal filament, one on either side of the median longitudinal axis, that are contiguous along their inner margins. A somewhat larger circular body is present, attached to the posterior surface of the two anteriormost bodies. An elongate, bifurcate body is attached to the posterior surface of the circular body; both distally rounded parts of the bifurcation extend posteriorly and slightly laterally into a larger semirectangular fourth part. The change in the shape of the organ from the preceding chalimus may be due to a shrinking of the structure, the anterior two parts being formed from the single ovoid structure present on the second chalimus; the semirectangular fourth part can not be traced to any definite

area in the frontal organ of the preceding stage. Yolk material is still visible in the alimentary tract and is concentrated in an enlarged area just posterior to the ocular region.

Eight specimens of the third chalimus lasted for approximately 33 hr at room temperature (approximately 23 C) at which time they moulted into the more elongate fourth chalimus.

The elongate condition of the fourth chalimus indicates a cyclic condition in the growth of the first four chalimus stages (Fig. 5). The average greatest length of the first chalimus (11 specimens), excluding setae, is 1.54 times the greatest width, of the second chalimus (45 specimens) is 2.04 times the width, of the third chalimus (25 specimens) is 1.54 times the width, and of the fourth chalimus (74 specimens) is 1.95 times the width. This cyclic tendency, from stubby to elongate to stubby to elongate, in the relationship between the greatest length and greatest width in the first four chalimus stages can not be explained by the growth of any single structure or body part. There appears to be a cyclic growth tendency in several body parts. For example, the cephalothorax length as a per cent of the total length is 79.1, 74.3, 79.5, and 73.6 for the first four chalimus stages respectively; the maximum width of the genital-abdominal segment as a per cent of the maximum length of the segment is 186.0, 153.6, 180.0, and 153.8 (genital segment only for this last measurement) for the first four stages respectively. Certainly, the inclusion of the second pedigerous segment into the cephalothorax affected the length of the cephalothorax as a per cent of the total length measurements in the second chalimus but the fact that the third pedigerous segment was included in the cephalothorax in the third chalimus did not appear to affect the trend in that stage.

The cephalothorax of the fourth chalimus (Fig. 9*d*) is ovoid in outline as in the preceding chalimus stages. The greatest length of the cephalothorax, including the frontal region but not the frontal filament, is slightly more than 1.3 times the greatest width. The frontal region and frontal plates are now distinct and the division of the region from the cephalothorax is complete. The division between the frontal region and the cephalothorax forms an irregular groove curving anteriorly from its origin on the anterior lateral margin. The anterior margin of the frontal region is broadly curved, the anterior lateral surfaces forming laterally projecting lobes, the posterior lateral margin connecting these lobes to the lateral margins of the cephalothorax. The lateral cephalothoracic margins are generally convex, although wavy; the posterior lateral corners are rounded. The lateral posterior margins, outside the posterior sinuses, are bilobed, consisting of the broadly rounded posterior lateral extensions of the lateral regions and the narrow, lobate lateral surface of the median thoracic area. The posterior sinuses are distinct and slender, generally V-shaped although sometimes U-shaped. The median thoracic area extends posteriorly well past the posterior extensions of the lateral regions and is irregularly tapered to the slightly rounded posterior margin. The lateral margins of the median thoracic area are continuous with the inner margins of the posterior sinuses. The major cephalothoracic grooves, as in the preceding stage, form an H. The anterior legs of the H, however, curve laterally from the junction with the cross groove anteriorly to their termination lateral and just posterior to the eyes. The lateral strengthening regions of the adult are not yet visible.

The free fourth pedigerous segment is short, its greatest length approximately two-thirds its width. The anterior end of the segment is overlapped by the posterior extension of the median thoracic area of the cephalothorax. The lateral margins taper both anteriorly and posteriorly from the widest point, in the middle of the segment, at the junction of the fourth thoracic legs. The posterior margin is distinct, forming a flatly convex groove.

The genital segment (Fig. 12*e*) is slightly shorter than the fourth pedigerous segment; its greatest length, excluding the slightly projecting fifth legs, is approximately two-thirds its width. The widest point is in the posterior medial region of the segment. The anterior lateral margins curve convexly, the posterior lateral margins concavely. The fifth legs project as dactyliform processes from the concave posterior lateral margins and extend slightly past the posterior end of the segment. The legs are tipped by two small plumose setae. The posterior margin of the segment is distinct although irregular.

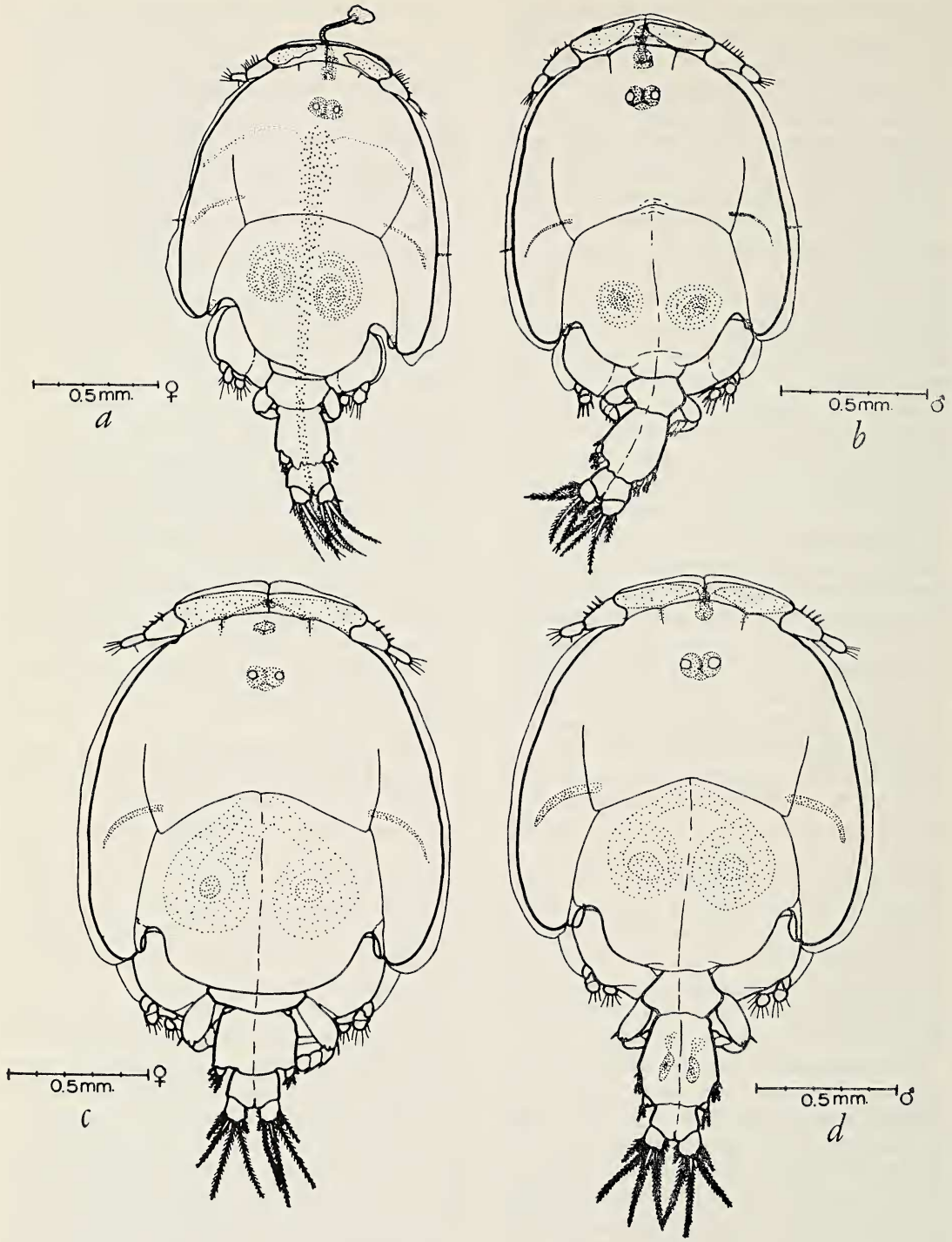

FIG. 10. Body of fifth and sixth chalimus developmental stages of *L. dissimulatus*. *a*, Dorsal view of attached female fifth chalimus; *b*, dorsal view of free-moving male fifth chalimus; *c*, dorsal view of free-moving female sixth chalimus; *d*, dorsal view of free-moving male sixth chalimus.

The abdomen (Fig. 12*e*) is slightly more than one-half the length of the genital segment; its greatest width is approximately twice the greatest length. The lateral margins are flatly convex or straight; the lateral posterior margins are slightly concave and taper to the median, bilobed anal region.

The bifurcate third part of the frontal organ (Fig. 13*e*) now extends to the posterior end of the smaller semirectangular fourth part. Both parts of the bifurcation are club-shaped and do not extend laterally as in the third chalimus. The alimentary tract is the same as that of the preceding stage although there is not as much yolk material.

Three specimens of the fourth chalimus lasted for about 36 hr under laboratory conditions (temperature approximately 23 C) before they moulted into the fifth chalimus.

The fifth chalimus (Fig. 10*a*, *b*) is found both attached and free on the host although more frequently attached. With the exception of a few structures such as the genital segment and some of the appendages, the somewhat flabby condition of the body and appendages characteristic of earlier chalimus larvae is absent and the stage is quite similar to the adult. The greatest length of the cephalothorax, including the frontal region, is approximately 1.3 times its greatest width, excluding the now present marginal flanges. The frontal plates form most of the frontal region and a narrow, membranous flange projects from its broadly curved anterior margin. The lateral frontal region surfaces project slightly, the posterior lateral margins connecting the lobate projecting portions to the lateral margins of the cephalothorax. The division between the cephalothorax and the frontal region is a distinct three-lobed groove, the median lobe of which is approximately twice the length of the lateral lobes. The lateral margins of the cephalothorax are broadly curved, with distinct marginal flanges extending from the junction of the frontal region posteriorly around the posterior extensions of the lateral regions to the beginning of the posterior sinuses. The lateral posterior margins, outside the posterior sinuses, are bilobed and consist of the rounded posterior extensions of the lateral regions and the sharply rounded lateral surface of the median thoracic area. The posterior sinuses are distinct and U-shaped. The median thoracic area extends posteriorly well past the posterior extensions of the lateral regions; its posterior margin is broadly rounded but possesses a small, median protrusion that forms the junction of the free fourth pedigerous segment in the now discernible male but which is absent in the female. The lateral margins of the protruding median thoracic area are continuous with the inner margins of the posterior sinuses. The major cephalothoracic grooves are similar to those of the preceding chalimus but appear more definite and not quite as irregular. Two heavily sclerotized regions, the lateral strengthening regions, are visible as posterior laterally curved, rodlike structures in the cephalothorax, originating just anterior and slightly medial to the junction of the longitudinal legs of the cephalothoracic grooves and extending to the region of the lateral margins.

The free fourth pedigerous segment is short; its greatest length is approximately one-half its greatest width. The posterior portion of the median thoracic area of the cephalothorax overlaps the anterior end of the segment slightly in the female but not in the male. The lateral margins are convex, the middle of the segment being the broadest region and slightly overlapping the proximal end of the fourth thoracic legs. The posterior margin is distinct although slightly irregular.

Because of the presence of the sixth thoracic legs on the male of this stage, the sexes can now be differentiated, as the female does not possess this appendage pair. As will be discussed later, the second antennae can not be used in differentiating the sexes of any of the chalimus stages of *L. dissimulatus*. The presence or absence of the sixth legs is the best method so far found by which the sexes can be told apart in both the fifth and sixth chalimus stages.

The genital segment of the female (Fig. 12*g*) is as wide as long; the lateral margins are flatly or broadly convex. The anterior end possesses two lateral, rounded protuberances that are distinct in a dorsal view but indistinct in a ventral view. The posterior lateral margins are indented, the lobate fifth legs arising from the ventral surface and projecting posteriorly. The fifth leg does not project past the posterior end of the genital segment as in the preceding stage. Four plumose setae, an additional two setae over the

last stage, are spaced along the outer margin of the fifth leg. The posterior margin of the female genital segment is broadly rounded in some specimens and irregular in others.

The male genital segment (Fig. 12*f*) is similar to that of the female although slightly longer; the lateral margins are, however, not indented in the dorsal view. Both the fifth and sixth legs arise from the posterior ventral lateral surface, adjacent to each other. Further, both legs are lobate, the sixth extending slightly past the division between the genital segment and abdomen. The fifth leg possesses one plumose setule on the outer base of the leg and two plumose setae on the distal end; the sixth leg is tipped by two plumose setules.

The abdomen (Fig. 12*f*, *g*) is bell-shaped and short; its greatest length is one-half that of the genital segment in the males, slightly longer in the females, and the greatest width is approximately 1¼ times the length. The posterior region of the single abdominal segment is broader than the anterior, the lateral margins are convex, and the lateral posterior margins are concavely tapered to the bilobed anal region.

The frontal organ (Fig. 13*f*) is similar to that of the preceding stage although the component parts are less distinct. The attachment filament, if present, arises from a circular indentation on the anterior ventral surface just anterior to the frontal organ. In unattached forms this circular indentation forms a scar which is the only evidence of the attachment filament. The yolk material that was present in the fourth chalimus now appears to be completely absent.

Only two specimens survived from the moult into the fifth chalimus to the moult into the sixth. Both of these specimens spent approximately 24 hr in the fifth chalimus stage under laboratory conditions (temperature approximately 23 C).

The sixth chalimus stage (Fig. 10*c*, *d*) is the last larval stage. Specimens in this stage of development were found both attached and free although, in contrast to the fifth chalimus, more frequently free. The greatest length of the cephalothorax, including the frontal region, is approximately 1.2 times the greatest width, excluding the marginal flanges. The frontal region is similar to that of the fifth chalimus. The lateral margins of the cephalothorax are broadly curved and are fringed with a distinct marginal flange. The posterior lateral corners of the cephalothorax are broadly rounded; the lateral posterior margins, outside the posterior sinuses, are bilobed, as in the preceding two stages, and consist of the rounded posterior extensions of the lateral regions and the sharply rounded lateral posterior surface of the median thoracic area. The posterior sinuses are distinct and U-shaped. The median thoracic area extends posteriorly slightly past the posterior extensions of the lateral areas. The posterior margin of the extension is broadly rounded in the female but has a flat median protrusion in the male. The lateral margins of the extended median thoracic area are continuous with the inner margins of the posterior sinuses. The major cephalothoracic grooves are similar to those of the preceding chalimus stage. Minor cephalothoracic grooves are visible on some specimens and, when present, extend posteriorly from the division between the frontal region and the cephalothorax. The lateral strengthening regions are proportionately larger than in the fifth chalimus but are similar in general shape and position.

The free fourth pedigerous segment is short, its length approximately one-half the width. The anterior end is covered by the posterior end of the median thoracic area of the cephalothorax in the female but not in the male. The middle of the segment protrudes laterally, the fourth thoracic legs being attached to the distal end of the protrusion; the segment tapers from the protrusion to the narrower anterior and posterior ends. The division between the fourth pedigerous segment and the genital segment is distinct although slightly irregular.

The genital segment of the female (Fig. 12*i*) is slightly longer than wide, its greatest width being approximately four-fifths of the length. The lateral margins are broadly convex, the anterior lateral surface forming an irregular, nodelike formation at the junction with the fourth pedigerous segment. The fifth legs arise from the lateral posterior ventral surface but do not extend to the posterior end of the segment; these structures are lobate in outline and possess three plumose setae along their outer margin and one on the distal surface. The seta on the distal surface possesses a minute swelling on the proximal outer margin (Fig. 12*j*) which is absent in

both the fifth chalimus and the adult but which was present on all of the female sixth chalimus specimens examined.

The genital segment of the male sixth chalimus (Fig. 12*h*) is longer than that of the female; the greatest width is approximately three-fourths the greatest length. The lateral margins are flatly convex, angled slightly from a swelling on the anterior lateral corner, comparable to the nodelike formation on the female, to the widest point in the region of the fifth legs. The posterior region of the segment curves medially from the region of the fifth legs to the abdomen. Both the fifth and sixth legs are lobate, the fifth approximately one-half the length of the sixth. The fifth legs project from the ventral lateral surface of the posterior one-half of the segment and possess a single plumose seta on the anterior end of the outer margin and three plumose setae on the distal surface, an increase of one seta from the fifth chalimus. The sixth legs project from the ventral surface just inside and posterior to the fifth legs and extend posteriorly to the posterior end of the segment. A single plumose seta, absent in the preceding chalimus, is present on the distal one-half of the outer margin of the sixth legs and two plumose setae are present on the distal surface.

The one-segmented abdomen of both sexes (Fig. 12*h*, *i*) is short, approximately one-third the length of the male genital segment; the length is exceeded somewhat by the width. The anterior end is slightly narrower than the posterior, the outer margin angled slightly from the anterior end to the middle of the segment. The posterior surface tapers from the middle of the segment to the bilobed anal region at the posterior extremity.

The frontal organ (Fig. 13*g*) appears to have degenerated from the previous stage and now consists of two oval bodies contiguous on the median longitudinal axis of the body just posterior to the division between the frontal region and the cephalothorax. These two bodies are connected to the frontal filament in attached forms or to the circular depression in unattached forms by a slender, rod-shaped structure. The digestive tract is the same as that of the preceding stage.

Only one specimen survived from the moult into the sixth chalimus to the moult into the adult. The time spent by this single specimen in the sixth chalimus was somewhere between 24 and 30 hr at a temperature of approximately 23 C.

After moulting from the sixth chalimus to the adult, the last moult in the life history, all of the appendages and processes remain unchanged. As seen in Figures 2–7, pertaining to the growth of *L. dissimulatus,* the maximum size of the male is almost completely attained by the sixth chalimus stage while that of the female not until the animal is well into the adult stage. Inasmuch as copulation takes place shortly after the terminal moult, the male would be more likely to be near its maximum size in the last larval stage. During the reproductive portion of the female's life, eggs are stored in the genital segment before they are extruded, causing this segment to swell considerably. As the female does not start to ovulate until some time after fertilization, the significant increase in size after the sixth chalimus is due, to a considerable extent, to the enlarged genital segment as is indicated in Figures 6 and 7. The presence of eggs in the genital segment also pushes the fifth legs laterally and, in some instances, obscures them in a dorsal view of the animal.

The cephalothorax of the adult female and male (Fig. 11*a*, *b*) is ovoid; the frontal region is distinct, separated from the cephalothorax by a trilobed groove. The lateral margins of the cephalothorax are convex and possess a distinct membranous flange. The posterior sinuses are distinct and of a shallow V-shape. The median thoracic region extends posteriorly slightly past the posterior extension of the lateral regions, forming the junction of the cephalothorax and the fourth pedigerous segment. The major cephalothoracic grooves are similar to those of the sixth chalimus; two minor grooves also extend posteriorly, for a short distance, from the junctions of the lateral and median lobes of the trilobed groove separating the frontal region from the cephalothorax. The rodlike strengthening regions are more heavily sclerotized than those of the sixth chalimus but are similar in shape and are in the same position.

The fourth pedigerous segment of the female and male is short; the lateral regions are drawn out at the fourth leg as in the preceding stage. The terminal portions of the lateral ex-

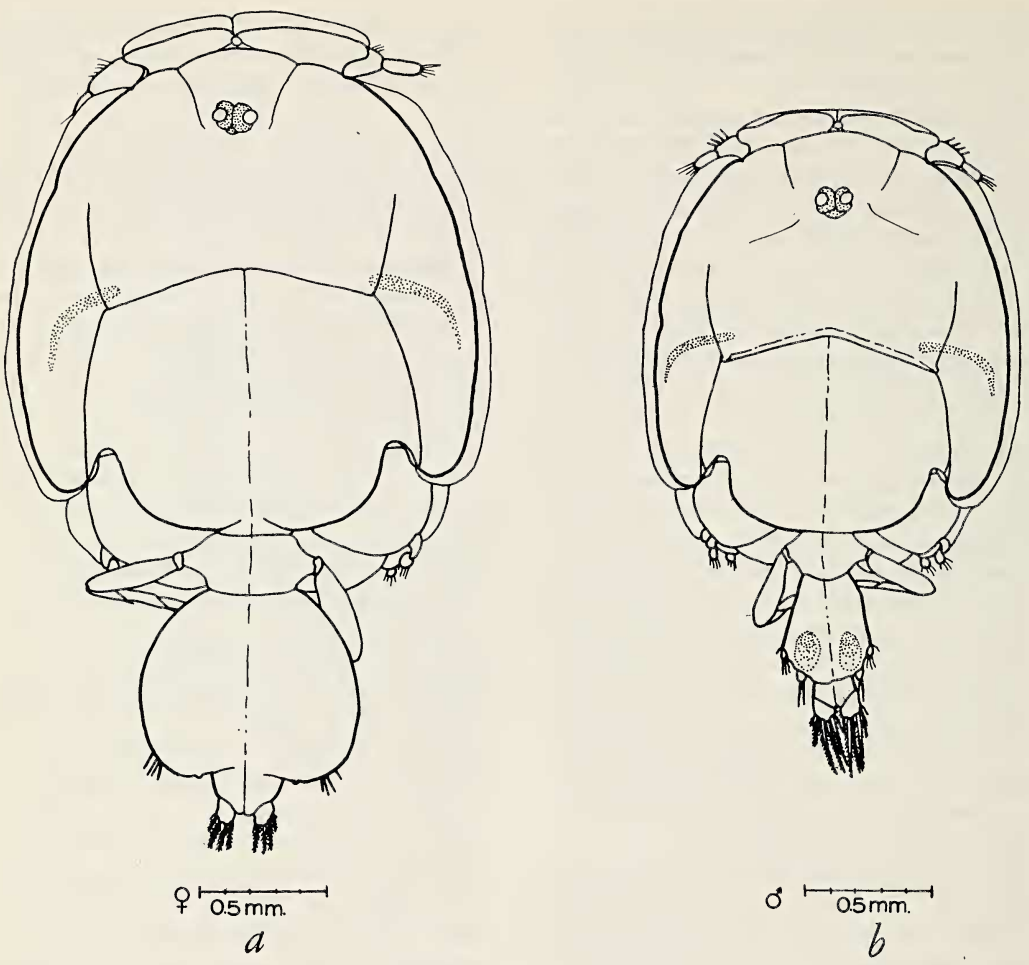

FIG. 11. Body of adult *L. dissimulatus*. *a*, Dorsal view of adult female; *b*, dorsal view of adult male.

tensions are cup-shaped and form socket-like attachments for the fourth legs. The division between the fourth pedigerous segment and the genital segment is distinct and curved convexly.

The shape of the female genital segment (Fig. 12*l*) is variable, dependent upon the number of eggs present in the segment. The segment is flaccid and ovoid in females that have recently extruded egg strings, and is almost circular in females whose genital segment is packed with eggs. Two small knoblike protrusions are present on the posterior margin lateral to the junction of the abdomen; these knobs are characteristic for the female of this species but are not present until the adult stage. The general shape of the fifth legs is similar to that of the sixth chalimus although the proximal seta of the three plumose setae present on the lateral surface of the leg of the preceding stage now arises from the surface of the genital segment, just lateral to the base of the fifth leg. The movement of this seta may be due to the swelling of the genital segment.

The genital segment of the male (Fig. 12*k*) is ovoid, the width slightly more than three-fourths the length. The shape of this segment and of both the fifth and sixth legs is very similar to that of the sixth chalimus male. The armature of the legs of both stages is identical.

The abdomen of the adult female and male is slightly longer than that of the sixth chalimus (0.12 mm average for 15 sixth chalimus speci-

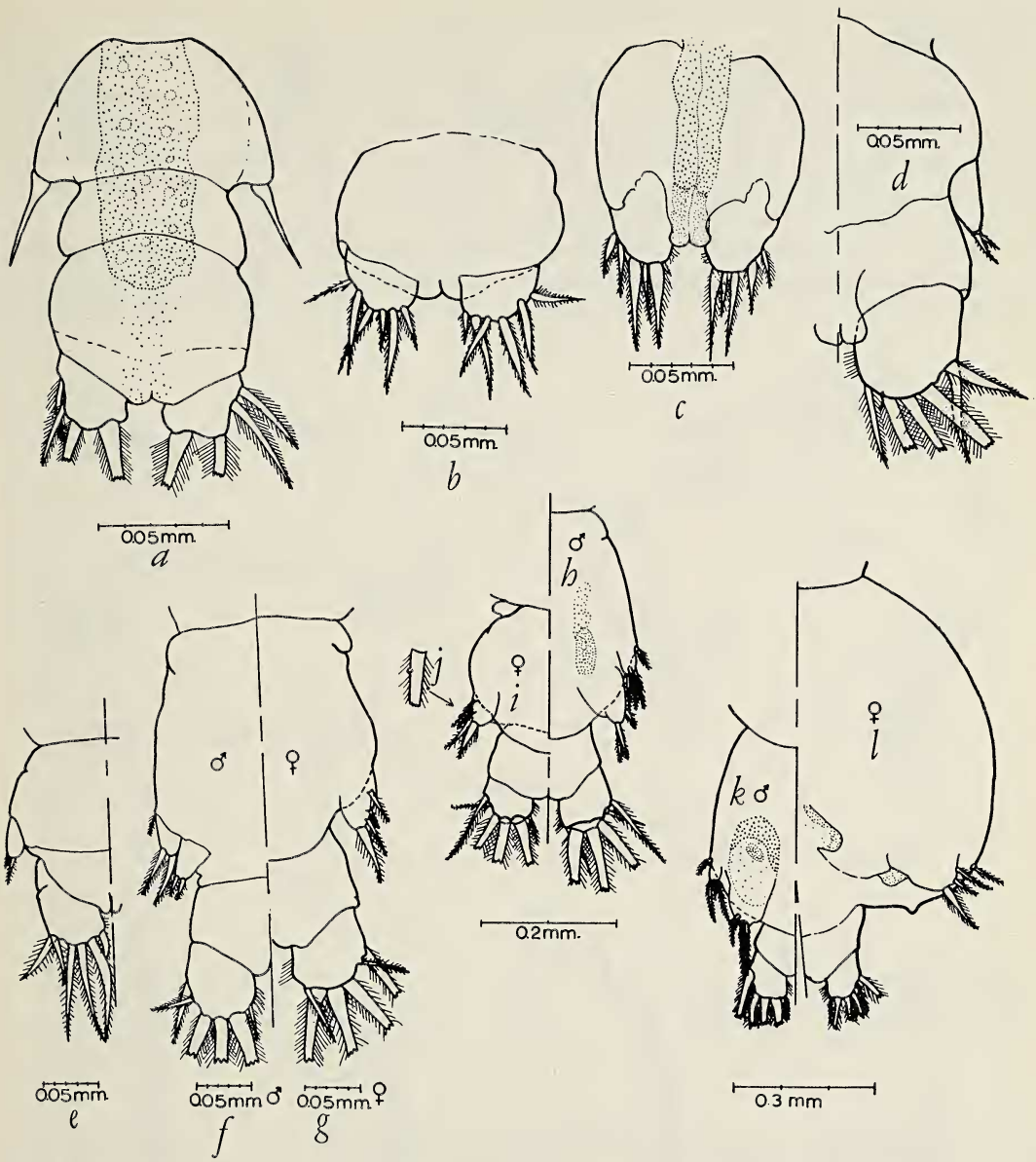

FIG. 12. Genital segment, abdomen, and caudal rami of developmental stages of *L. dissimulatus*. *a,* Copepodite, ventral view showing third and fourth pedigerous segments, genital-abdominal segment and caudal rami; *b,* first chalimus, ventral view of genital-abdominal segment and caudal rami; *c,* second chalimus, ventral view of genital-abdominal segment and caudal rami; *d,* third chalimus, ventral view of genital and abdominal segments, fifth leg and caudal rami; *e,* fourth chalimus, ventral view of genital and abdominal segments, fifth legs and caudal rami; *f,* male fifth chalimus, ventral view of genital and abdominal segments, fifth and sixth legs and caudal rami; *g,* female fifth chalimus, ventral view of genital and abdominal segments, fifth legs and caudal rami; *h,* male sixth chalimus, ventral view showing genital and abdominal segments, beginning of internal spermatophore, fifth and sixth legs and caudal ramus; *i,* female sixth chalimus, ventral view showing genital and abdominal segments, fifth legs and caudal ramus; *j,* enlarged distal seta of female fifth leg showing node on outer proximal surface; *k,* adult male, ventral view of genital and abdominal segments, fifth and sixth legs and caudal ramus; *l,* adult female, ventral view of genital and abdominal segments, fifth legs and caudal ramus.

mens, 0.14 mm average for 30 adult specimens). The general shape, however, is the same.

The frontal organ in the adult (Fig. 13*b*) is greatly reduced, being visible only as a small opaque area on the median longitudinal axis of the body just posterior to the groove dividing the frontal region from the cephalothorax. The attachment filament is completely absent, the only indication of its previous presence being the circular scar mentioned with reference to unattached specimens of the sixth chalimus.

Antennule

Throughout development, from the nauplius to the adult, the antennule is two-segmented. The changes that occur in this appendage are changes in the general shape and relative size of the segments in addition to changes in the armature.

The antennule of the first nauplius (Fig. 14*a*) is uniramous and is attached to the anterior ventral lateral surface of the body. The lateral

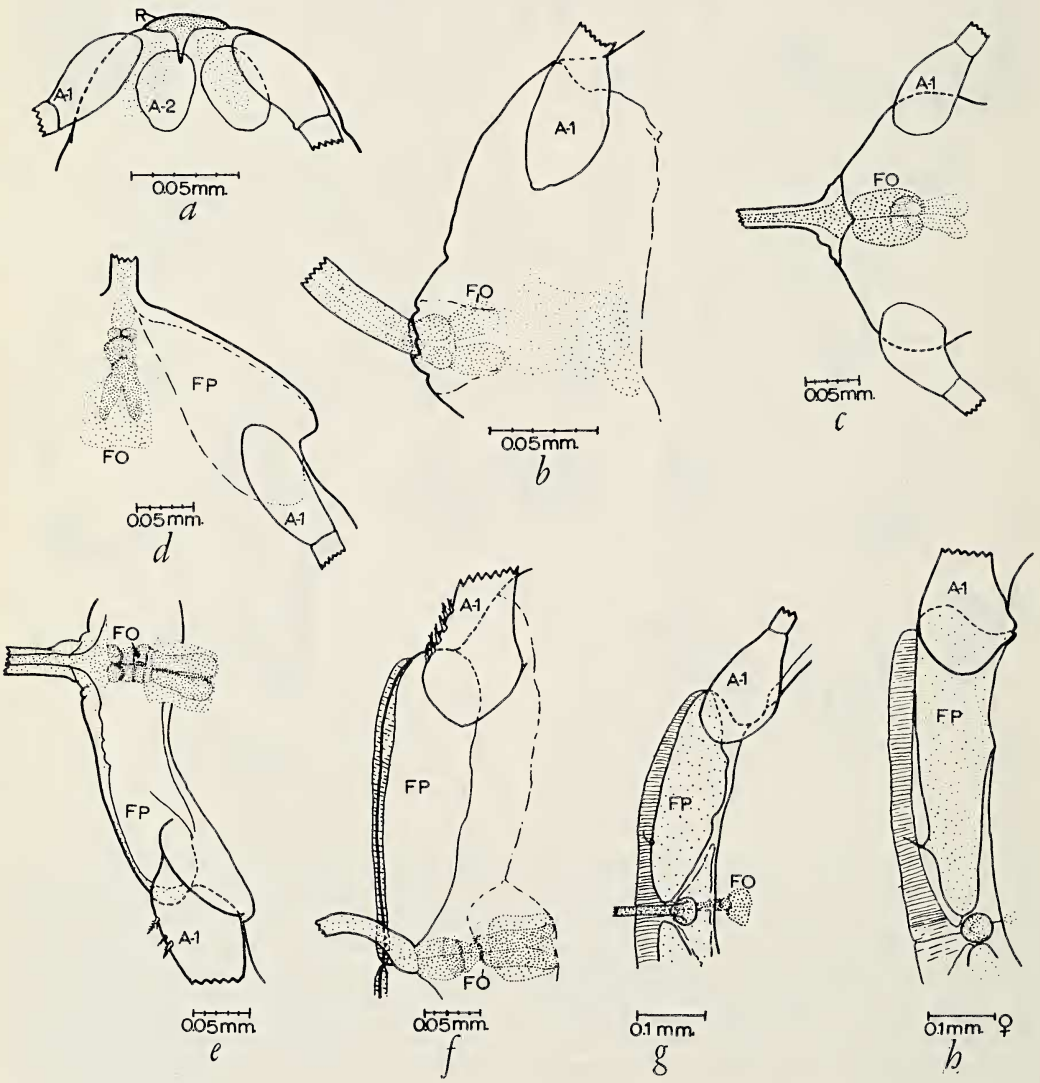

FIG. 13. Frontal region of developmental stages of *L. dissimulatus*. Ventral view of anterior surface: *a*, Copepodite; *b*, first chalimus; *c*, second chalimus; *d*, third chalimus; *e*, fourth chalimus; *f*, fifth chalimus; *g*, sixth chalimus; *h*, adult. *A-1*, Antennule; *A-2*, base of second antenna; *FO*, frontal organ; *FP*, frontal plate; *R*, Rostrum.

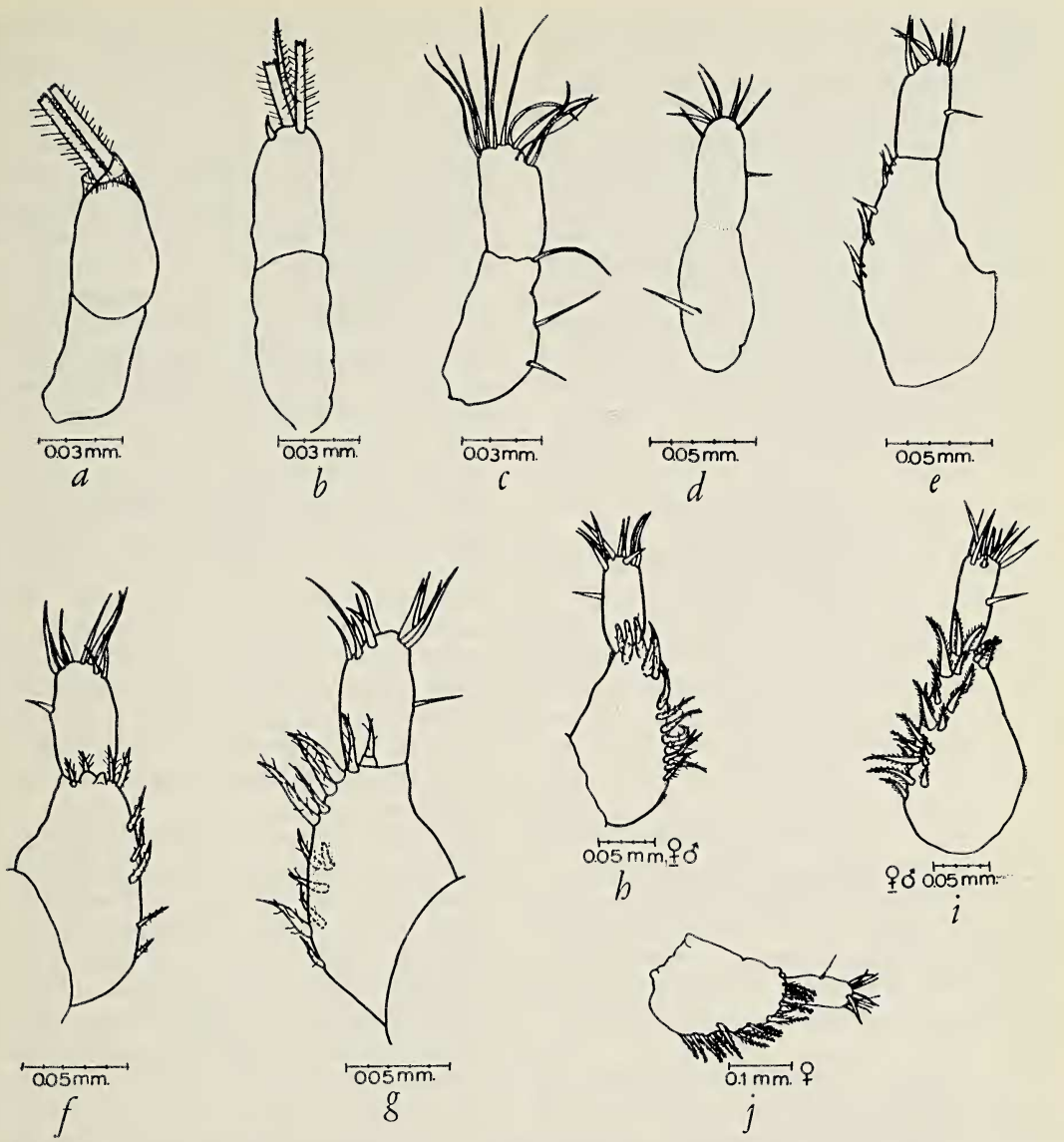

FIG. 14. Antennule of developmental stages of *L. dissimulatus* (ventral view). *a*, First nauplius; *b*, second nauplius; *c*, copepodite; *d*, first chalimus; *e*, second chalimus; *f*, third chalimus; *g*, fourth chalimus; *h*, fifth chalimus; *i*, sixth chalimus; *j*, adult.

margins of both segments are slightly irregular, more so in some specimens than in others. The first segment is slightly shorter than the second and is tapered rapidly in the proximal one-third to the narrow proximal end, the surface of attachment with the body. The second segment is tapered from the proximal to the slightly narrower, rounded distal end. The distal end of the second segment is encircled by a membrane projecting slightly past the segment. A broadly angled, heavily sclerotized process projects from the inner portion of the distal end of the second segment and two lightly plumose setae project from the inner portion of the distal end, adjacent to the process; these setae are slightly longer than the greatest length of the appendage.

The antennule of the second nauplius (Fig. 14*b*) is attached to the anterior ventral lateral

surface of the body. The first segment is now slightly longer than the second and its proximal end is almost pedunculate. The lateral margins of the segment are irregular although basically parallel; the distal end is slightly convex. The second segment possesses two long, lightly plumose setae, as in the first nauplius, but also a short, lightly plumose seta from the inner distal margin in addition to one short, spinelike process on the outer distal surface. The membrane present on the preceding stage is completely absent. The copepodite antennule is visible in late second naupliar specimens, incompletely filling the appendage; the character of the copepodite appendage is, however, not definable.

The antennule of the copepodite is attached to the ventral lateral surface just lateral to the rostrum. The first segment is almost 1⅓ times the length of the second; its greatest width is approximately one-half the greatest length. The proximal anterior lateral margin (the margin that faces anteriorly in situ) of the first segment is strongly convex; the remaining lateral margin and the posterior lateral margin are somewhat irregular. The first segment possesses two naked setae from the middle of the anterior margin and one naked seta from the anterior distal margin. The division between the first and second segments is distinct although slightly irregular. The greatest length of the second segment is slightly less than the greatest width, the lateral margins are almost parallel, and the distal margin is irregular. The second segment gives rise to 11 naked setae from its distal surface.

The division between the two segments of the first chalimus antennule (Fig. 14*d*) is indistinct; the appendage is attached to the anterior ventral lateral surface just anterior to the indistinct, incomplete ventral groove dividing the frontal region from the cephalothorax. The first segment is slightly more than 1½ times the length of the second, and the proximal region is broader than the distal; the rounded proximal end is almost included in the posterior margin, and the anterior and posterior margins are irregularly convex. A single naked seta is present on the proximal one-half of the anterior surface. The second segment is approximately twice as long as wide, the posterior and anterior margins are generally flatly convex, and the distal end is rounded. A single naked seta is present on the middle of the posterior margin, as in the adult; eight naked setae are also present on the distal end.

The first chalimus antennule shows some degeneration from the copepodite appendage. This condition is evident in most of the appendages in the change that occurs from the copepodite to the first chalimus.

The division between the two segments of the second chalimus antennule (Fig. 14*e*) is distinct. The first segment is approximately twice the length of the second, comparatively longer than in the preceding stage. The proximal end of the first segment is broad; the segment is tapered irregularly to the narrower distal end. The anterior lateral margin is smoothly convex, longer than the irregularly concave posterior margin; the distal margin is flat. About 10 naked setules are present along the anterior lateral margin of the first segment. The second segment is twice as wide as long, the lateral margins are slightly irregular, and the distal margin irregularly rounded. A single naked seta is present on the middle of the posterior margin of the second segment in addition to nine naked setae on the distal surface.

The third chalimus antennule (Fig. 14*f*) is attached to a swelling on the posterior lateral portion of the tear-shaped frontal region. The greatest length of the first segment is about twice that of the second; its greatest width is two-thirds the length. The proximal end of the segment is angled; the anterior margin is thus more than twice the length of the posterior; the distal end is irregular and has two distinct swellings. Six lightly plumose setae arise from the anterior margin of the first segment and three from the distal margin. The second segment is slightly constricted at the junction of the first segment and curved convexly distally, causing the segment to appear club-shaped. The greatest width of the second segment is slightly more than one-half the length. As in the preceding two chalimus stages, a single naked seta is present on the middle of the posterior margin and nine naked setae arise from the distal surface.

The fourth chalimus antennule (Fig. 14*g*) is also attached to a swelling on the posterior lateral corner of the frontal plates which are now oriented more in a horizontal manner than

in the third chalimus. The general shape of the two antennular segments is similar to that of the preceding stage although the two distinct swellings present on the distal end of the first segment are now absent. The anterior surface of the first segment bears 10 setae that are distinctly plumose; the anterior distal surface bears two plumose setae. The second segment bears a single naked seta from the middle of the posterior margin, four from the posterior distal surface, and six from the anterior distal.

The antennule of the fifth chalimus (Fig. 14*h*) is attached in the same region as that of the fourth although the swelling at the junction of the appendage and the frontal region is not as distinct. The overlap of the antennule base onto the anterior ventral surface of the cephalothorax (see Fig. 13*e–h*) in the fifth and sixth chalimus and the adult may be due, at least in part, to the incorporation of the swollen portion of the frontal region into the frontal region of later stages and the resultant displacement of the posterior portion of the antennule base onto the cephalothorax. The attachment of the antennule thus appears to be basically on the frontal region and secondarily on the cephalothorax. The first segment of the fifth chalimus antennule is, with regard to the second segment, slightly longer than in the preceding stage, being more than twice the length of the second segment. The greatest width of the segment is slightly more than 1½ times the length; the anterior margin is flatly convex medially and broadly rounded distally and proximally. The posterior margin is irregular, with a slight angular protrusion from the distal region. The anterior surface of the first segment bears 16 plumose setae, the distal surface three. The length of the second segment is approximately 2½ times the width, the lateral margins are flatly convex, and the distal margin is rounded. The armature of this segment is the same as in the preceding stage.

The antennule of the sixth chalimus (Fig. 14*i*) is attached to the ventral lateral surface of the frontal region and is adjacent to or slightly overlaps the anterior ventral surface of the cephalothorax. The second segment is slightly longer than that of the preceding stage. The first segment is broad proximally, its greatest width being approximately five-eighths of the greatest length, and tapers to the narrow distal end. The anterior margin is irregular except for the broadly convex proximal region, the posterior margin is shorter than the anterior, and the posterior surface bears a small distal protrusion. Nineteen plumose setae arise from the anterior surface of the first segment and the rounded distal surface bears five more. The second segment is club-shaped; the greatest width is slightly more than one-third the length. The lateral margins are generally flatly convex, the proximal end slightly narrower than the rounded distal end. The armature of the second segment consists of one naked seta from the middle of the posterior margin and 11 naked setae from the distal surface.

The antennule of the adult (Fig. 14*j*) is similar to that of the sixth chalimus except for the armature. The first segment has a small bifurcate protrusion on the posterior distal corner, the spines of which are crenate in the female and dentate in the male. The first segment bears 20 plumose setae on its anterior and distal surfaces; the second segment bears one naked seta on the middle of the posterior surface and 12 naked setae on the distal surface.

Second Antenna

In contrast to the antennule, the second antenna changes drastically during the life cycle of *L. dissimulatus,* from a biramous swimming appendage in the nauplius to a uniramous prehensile appendage in the adult.

The second antenna of the first nauplius (Fig. 15*a*) is biramous and attached to the ventral lateral surface just posterior to the base of the antennule. The protopodite is one-segmented, its greatest width approximately three-fourths of the greatest length. The lateral margins, except at the proximal end, are almost parallel; the distal margin is broadly curved. The five-segmented exopodite arises from the dorsal lateral surface of the protopodite, not from the distal end; the division between the exopodite and the protopodite is indistinct and incomplete. The first exopodite segment is slightly longer than the second, its proximal region tapered evenly to the narrow distal end. The second segment is tapered evenly from the proximal to the narrow distal end; a single lightly plumose seta is present on the inner distal lateral

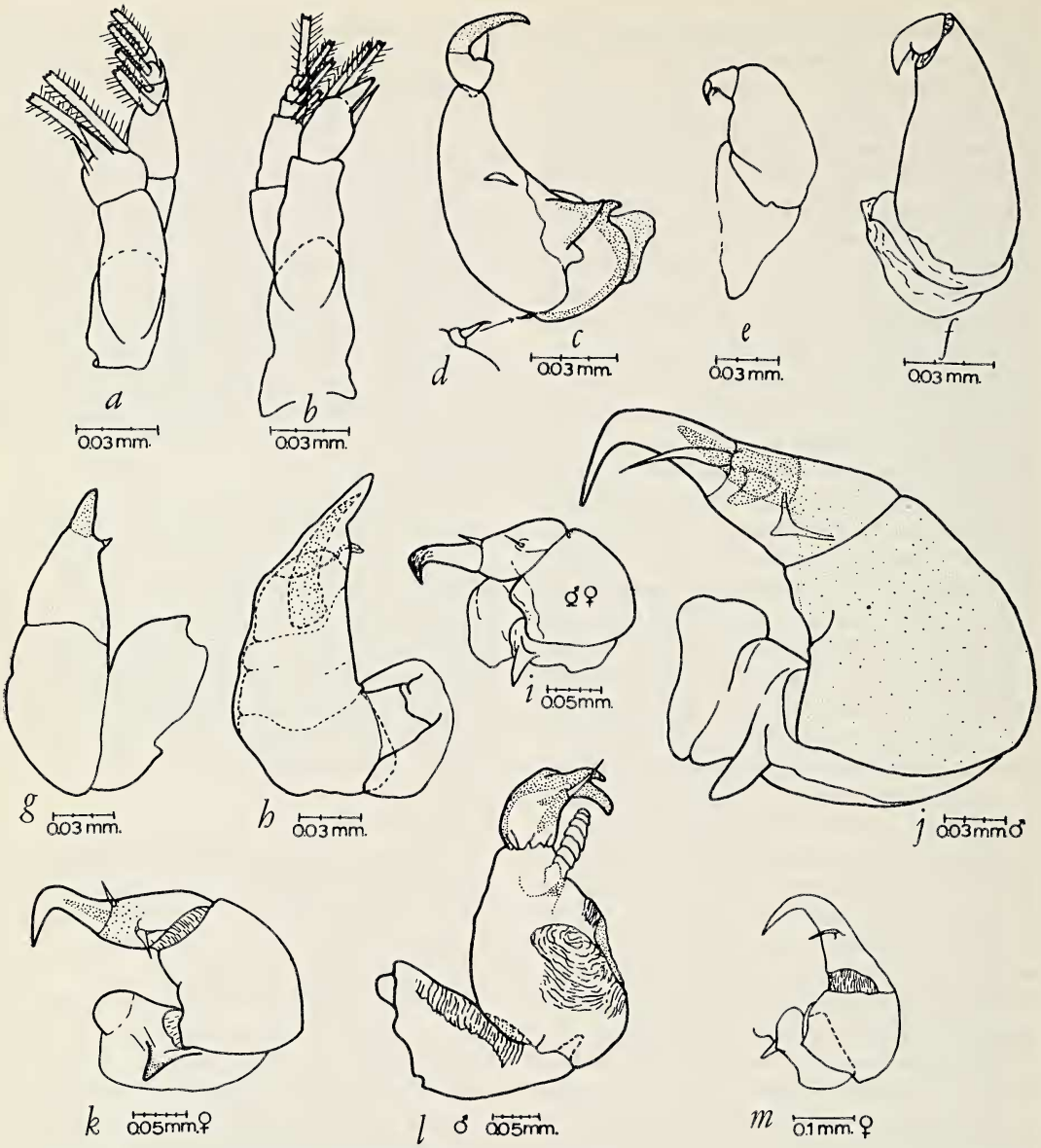

FIG. 15. Second antenna of developmental stages of *dissimulatus*. *a*, First nauplius, ventral view; *b*, second nauplius, ventral view; *c*, copepodite, posterior surface; *d*, setule of first segment of copepodite antenna (enlarged over original enlargement); *e*, first chalimus, posterior surface; *f*, second chalimus, posterior surface; *g*, third chalimus, posterior surface; *h*, fourth chalimus, posterior surface; *i*, fifth chalimus, posterior surface; *j*, male sixth chalimus, posterior surface; *k*, female sixth chalimus, posterior surface; *l*, male adult, posterior surface; *m*, female adult, posterior surface.

surface. The third segment is slightly more than one-third the length of the second; it is slightly wider distally than proximally and possesses a spinelike projection on the anterior proximal surface that extends distally slightly past the end of the segment. Further, the third segment gives rise to a single lightly plumose seta from the inner lateral surface. The fourth segment is similar to the third although slightly smaller. The fifth segment is minute, its distal surface slightly irregular; the anterior lateral margin is longer than the posterior; a single lightly plu-

mose terminal seta is borne by this segment. The endopodite is two-segmented and attached to the ventral lateral surface of the protopodite. The division between the endopodite and protopodite is also indistinct and incomplete. The first segment is about 3 times the length of the second; its proximal end is narrow and the segment is curved slightly to the broader distal end. The lateral and distal margins of the second segment are continuous and form a broadly rounded margin. A strong spinelike projection is present on the middle of the distal end of the second segment and a slender spinelike projection is present on the posterior distal end. The second segment also bears two lightly plumose setae from its anterior distal surface.

The second antenna of the second nauplius (Fig. 15*b*) is similar to that of the first nauplius in general outline and make-up. The spinelike projections on the third and fourth segments of the first nauplius exopodite are absent in the second although the remaining armature is the same. The make-up and armature of the two endopodite segments is the same as that of the preceding stage with one exception: the two spinelike processes on the distal surface of the second segment appear to be more strongly developed.

The second antenna of the copepodite (Fig. 15*c*, *d*) is uniramous and three-segmented. The appendage is attached to the anterior ventral surface just medial to the posterior edge of the antennule base. Wilson (1905:542) indicates that the caligid second antenna is still biramous in the copepodite stage and Heegaard (1947: 56, fig. 14) describes and figures the reduced exopodite on the second antenna of *Caligus curtus*. Unless the small setule (Fig. 15*d*) or one of the projections on the proximal segment of the second antenna of *L. dissimulatus* is the remnant of the now absent ramus of the biramous second naupliar appendage, no evidence of a biramous condition is present. The first segment of the copepodite appendage is short and irregular, folded in several places, and possessing two backward-projecting, broadly-angled, spinelike processes, the proximal of which is poorly developed and the distal well developed. The division between the first and second segments is distinct although irregular. The second segment is broad proximally but tapered to a narrow distal end; the lateral margins are regular, the distal surface concave. The second segment possesses a small lappet-like process projecting from the middle of the posterior medial surface. The third segment is short, less than one-eighth the length of the second; the proximal end is slender, the distal is broad, and both lateral margins are convex. The distal end of the third segment is flat except for a slight depression in the middle. A large spinelike terminal process curves anteriorly from the posterior one-half of the surface; a slender, seta-like accessory process projects from the anterior surface.

The first chalimus second antenna (Fig. 15*e*) appears to have degenerated somewhat; its shape is rather indistinct and the entire appendage appears flabby. The second antenna of this stage is attached just posterior and medial to the antennule base. The first segment is broad proximally, somewhat narrower distally, and the general outline is irregular. The distal end of the first segment forms an articulation surface for the second segment. The second segment is well developed; its greatest length is slightly more than the combined lengths of the first and third segments. This segment is broader proximally than distally, and the lateral margins are irregular, the outer longer than the inner; the distal surface faces inwards and its margin is generally flat. The third segment is short and truncate, tipped by a sharply curved, heavily sclerotized, spinelike process; the accessory process is present as a small seta-like structure on the distal one-half of the inner surface of the segment.

The second chalimus second antenna (Fig. 15*f*) is attached just posterior and medial to the base of the antennule. The first segment is broad and irregular in outline; its distal surface forms an articulation surface for the second segment. An indistinct, posteriorly directed, distally pointed process is present on the inner surface of the segment. The second segment is well developed, twice the length of the combined first and third segments. This segment is broad proximally and tapers to a narrow distal end. The outer lateral margins are smoothly convex, the inner irregularly concave; the distal surface is angled towards the inner proximal end, and the distal margin is slightly irregular. The outer margin of the third segment is convex and continuous with the outer margin of the short, in-

wardly curved terminal process. The inner margin of the third segment is broken by the lobe-shaped proximal region. The division between the terminal process and the segment is indistinct. In addition to the terminal process, a small seta-like accessory process is present on the lobate inner proximal region.

The second antenna of the third chalimus (Fig. 15*g*) appears to have degenerated even more when compared with the same appendage on the copepodite and the previous two chalimus stages. This condition is a continuation of the trend initiated in the first chalimus, a gradual loss of rigidity and distinct form before the development of the adult appendage. To exemplify this loss of form, the segments of the third chalimus appendage are distinct but plastic in nature, the integument is flabby, and the ridges and grooves present on the second antenna of one side of a specimen are often absent on the other; further, the sclerotization of the terminal process appears reduced. The greatest length and width of the first and second segments of the second antenna of the third chalimus are approximately equal although the shape is different. The distal end of the first segment is generally concave, of the second segment almost flat. The third segment is slightly shorter than either of the preceding two and is tapered from the broad proximal to pointed distal end. The inner margin of the segment possesses a distinct protrusion on the distal one-half that is tipped by a short, pointed process. The more heavily sclerotized terminal process of the succeeding stage is visible inside the distal portion of the third segment.

The second antenna of the fourth chalimus (Fig. 15*h*) is similar in general make-up to that of the preceding stage except that the first segment is not as long. Further, it has a flaplike structure projecting distally from the proximal end; one specimen also possessed a triangular, distally directed flap that appeared to correspond to the posteriorly directed, pointed process on the first segment of the adult female. The length of the second segment is greater than that of the first, the division between the second and third segments is indistinct, and the lateral margins of both segments are irregular. The distal inner margin of the third segment bears a small, lobate process that will become the accessory process of the adult and is the protrusion that was present on the same region of the previous stage. The distal end is bluntly pointed, more heavily sclerotized than the preceding stage but not as heavily as the terminal process of the fifth chalimus, visible inside the fourth.

The second antenna of the female and male fifth chalimus (Fig. 15*i*) are similar. The general appearance of the adult female appendage is now beginning to manifest itself in the females of this stage. The first segment is irregular, the distal surface concave and forming the articulation surface for the second segment. A spinelike, posteriorly directed process is present on the posterior surface of the segment. The second segment is short and strongly developed; the inner margin is convex, approximately 3 times the length of the concave outer margin due to the angled distal and proximal surfaces. The distal surface of the second segment is irregular; the inner portion is concave, the outer convex although both portions are heavily sclerotized and form the articulation surface for the third segment. The third segment and terminal process in both sexes is approximately 1½ times the length of the second segment; the proximal surface is lobate and articulates in the concavity of the distal end of the second segment. The terminal process of the third segment is curved inwards strongly at the distal end; the division between the process and the segment is indistinct. Further, two seta-like accessory processes are now present, one on the posterior proximal region, the second on the inner distal region.

The second antenna of the sixth chalimus (Fig. 15*j*, *k*) is similar in both sexes. The first segment is slightly longer in the male but, for both male and female, is short and the entire distal surface is concave, forming an articulation surface for the second segment. The first segment is irregular in outline, the outer surface appearing platelike and tapered gradually to the distal surface, the inner surface somewhat irregular, with a posteriorly directed, spinelike projection that is more distinct than in the previous stage. The second segment is strongly developed, its greatest width slightly more than four-fifths of the greatest length; the outer margin is flatly convex, longer than the irregularly concave inner margin. The width of the distal

end of the second segment is slightly less than three-fourths of the width of the proximal end; the distal surface is concave with its outer portion heavily sclerotized and serving as the articulation surface for the outer proximal end of the third segment. The third segment and terminal process are similar to those of the preceding stage although the process is slightly longer and the distal portion more sharply curved. The adult female and male appendage is visible within the second antenna of late sixth chalimus specimens. Both parts of the bifurcate terminal process of the adult male can be seen (Fig. 15*j*) as well as the single female terminal process (Fig. 15*k*).

It was earlier stated that the second antennae can not be used to differentiate the two sexes in the late chalimus of *L. dissimulatus*. As was just described, the female and the male second antenna are similar in the sixth chalimus, the last larval stage. Not until the moult from the sixth chalimus to the adult is there any significant difference between the appendages of the two sexes in *L. dissimulatus*. For this reason, the presence or absence of the sixth legs, found only in the male, was used as the major differentiating characteristic. Additionally, in the sixth chalimus, the presence of internal spermatophores in the male was used to verify the differentiation of the two sexes.

The second antenna of the adult (Fig. 15*l, m*) is attached to the ventral surface of the cephalothorax just anterior and medial to the postantennal process and posterior and lateral to the base of the antennule. The first segment of the female is short and forms a broad articulation surface for the second segment. The segment possesses a posteriorly directed, spinelike projection from the posterior proximal surface. The second segment is strongly developed, its greatest width being equal to its greatest length. The third segment is slender and heavily sclerotized, bearing a sharply curved, spinelike terminal process and two naked, seta-like accessory processes, one from the inner surface of the proximal region and the second from the distal lateral surface. The division between the third segment and terminal process is indistinct and incomplete.

The first segment of the adult male second antenna (Fig. 15*l*) is longer than that of the female; the segment is broader proximally than distally and is attached to the cephalothorax along the entire length of the proximal surface. The distal end of the first segment is small and two-pronged, forming an articulation surface for the second segment. Additionally, the major portion of the outer lateral surface forms an adhesion surface of heavily sclerotized, overlapping, platelike structures. The second segment is strongly developed, its greatest width slightly more than one-half of the greatest length. The outer margin of the segment is strongly convex proximally; the inner margin is irregular due to the presence of two sets of adhesion surfaces similar to those of the first segment. The inner distal margin of the second segment also possesses a finger-like protrusion that appears to be segmented but presumably forms an adhesion surface, and the segmented appearance is due to the overlapping plates. The protrusion is, in most specimens, curved around the second segment and appears as a regular adhesion surface but it is not attached to the segment except at its proximal end. The third segment is short and bears a bifurcate terminal process in addition to a single, naked, seta-like accessory process from the inner distal end.

Mandible

Comparing the over-all development of the three naupliar appendages, it is evident that the mandible has the most drastic change. Almost all of the change occurs in the moult from the second nauplius to the copepodite when the appendage changes from a biramous appendage to a uniramous, four-parted, rodlike process. The four-parted condition could not be traced to either the exopodite or the endopodite of the naupliar appendage. All four parts appear to be almost completely fused; there are no muscles penetrating the appendage and there is no trace of the second ramus of the biramous naupliar appendage. These three conditions make the analysis of the derivation of the mandible of the copepodite of *L. dissimulatus* extremely difficult, and even with the analysis made by Heegaard (1947:59, 196–202), no hypothesis can be offered until further work has been done.

The mandible of the first nauplius (Fig. 16*a*) is biramous and attached to the ventral lateral surface just posterior to the second antenna.

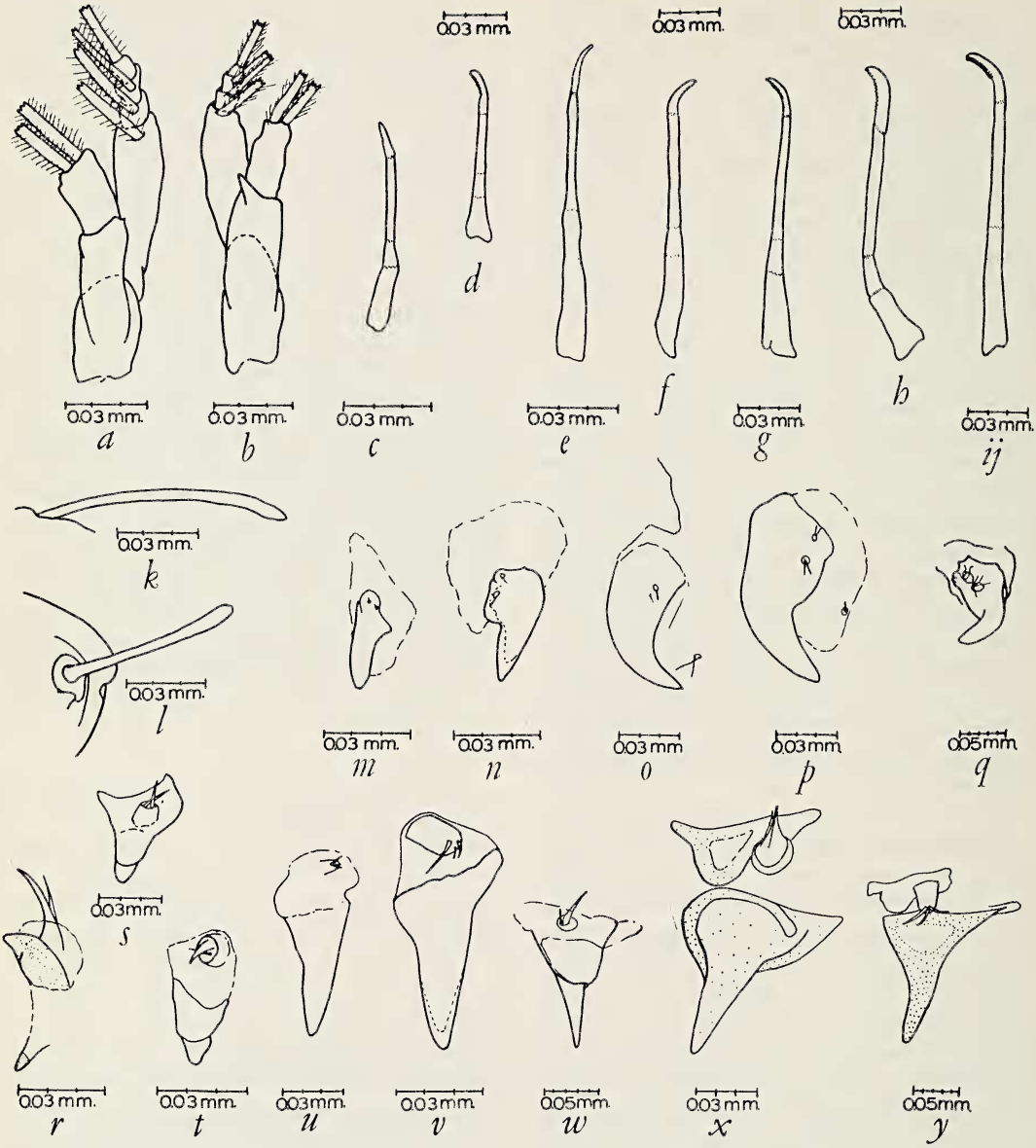

FIG. 16. Mandible, postantennal and postoral processes of developmental stages, in addition to balancers of naupliar stages of *L. dissimulatus*. *a–j*, Mandible: *a*, First nauplius, ventral view; *b*, second nauplius, ventral view; *c*, copepodite; *d*, first chalimus; *e*, second chalimus; *f*, third chalimus; *g*, fourth chalimus; *h*, fifth chalimus; *i*, *j*, sixth chalimus and adult. *k*, *l*, Nauplius balancers: *k*, First nauplius, dorsal view; *l*, second nauplius, lateral view (also posterior end of body of nauplius). *m–q*, Postantennal process: *m*, Third chalimus; *n*, fourth chalimus; *o*, fifth chalimus; *p*, sixth chalimus; *q*, adult. *r–y*, Postoral process: *r*, Copepodite; *s*, first chalimus; *t*, second chalimus; *u*, third chalimus; *v*, fourth chalimus; *w*, fifth chalimus; *x*, sixth chalimus; *y*, adult.

The protopodite is one-segmented, its greatest width about three-fourths of the greatest length; the lateral margins are slightly irregular although generally convex, and the distal margin is broadly curved. The exopodite is four-segmented and attached to the dorsal lateral surface of the protopodite although the division between the first segment and the protopodite is incomplete. The first segment of the exopodite is more than 2½ times the combined lengths of the remaining three segments, its lateral margins are broadly convex, and the distal surface has a concavity in which the proximal end of the second segment is attached. A single lightly plumose seta is present on the distal portion of the inner lateral surface of the first segment. The second segment is short, its greatest width about equal to the greatest length; the distal surface is slightly concave and receives the proximal end of the third segment. A single seta is present on the distal portion of the inner lateral surface of the second segment. The third segment is slightly longer than the second and flared from the narrow proximal to broader distal end; the distal surface also has an irregular concavity for the proximal end of the fourth segment. A single seta is present on the distal portion of the inner lateral surface of the third segment. The fourth or terminal segment is minute and rodlike, with a concave distal surface that receives the base of the slightly plumose terminal seta. The endopodite is two-segmented and attached to the ventral lateral surface of the protopodite although the division between the first segment and the protopodite is incomplete. The first segment is approximately 1⅓ times the length of the second, the lateral margins are slightly irregular, and the distal end is flared slightly and bearing a small, pointed protrusion on the anterior distal corner. The second segment has slightly irregular lateral margins, the distal end is slightly broader than the proximal, and the distal surface is flat and bears two lightly plumose setae.

The mandible of the second nauplius (Fig. 16*b*) is similar to that of the first nauplius. The first segment of the exopodite is, however, longer than that of the preceding stage, being more than 3½ times the combined lengths of the remaining three segments. The small pointed protrusion on the anterior distal corner of the first endopodite segment of the first nauplius is larger in the second nauplius and projects anteriorly although there is some variation in size in different specimens.

The copepodite mandible (Fig. 16*c*) is uniramous and four-parted as in the adult. The appendage is attached to the ventral surface of the cephalothorax just lateral to the division between the well-developed membranous hyperstome and hypostome and projects through the division into the mouth cone. All four parts are heavily sclerotized and indistinctly divided, the division often appearing only as a light area. The first part is approximately twice the length of the second, tapered slightly from the proximal to the narrower distal end. The second part is strongly tapered from the first to slender third part. The third part is elongate, the length slightly less than the combined lengths of the first two parts; the lateral margins are almost parallel. The fourth part is short, the length less than one-half that of the third part. The fourth part is also angled medially; there is no curvature as the fourth part of later stages has. The fourth part is tapered to a sharp point distally; the inner margin is lightly serrated but does not have the denticulations visible in the adult.

The condition exhibited by the copepodite mandible is changed but little in the chalimus stages. The only part that changes to any extent is the fourth part, the other three changing only slightly in their relative lengths. A slight curvature of the fourth part is visible in the first chalimus (Fig. 16*d*), this curvature becoming greater throughout the remaining chalimus stages (Fig. 16*e–i*) so that the fourth part is evenly curved in the sixth chalimus and adult (Fig. 16*i, j*). Further modification of the fourth part is from the sharply pointed condition of the copepodite to the bluntly rounded tip of the adult and the gradual appearance of the denticulations present on the inner surface of the adult.

Mouth Cone

The mouth cone is first exhibited by the copepodite, although a slight swelling is visible on the second nauplius that may be the beginning of this structure. The cone itself is formed of two membranous structures, a hyperstome and hypostome, that are usually closely applied

to each other or overlap slightly. A slight opening is visible in the proximal portion through which the mandibles project into the cone. Relatively little change occurs in the mouth cone from the copepodite to the adult although because of the size and nature of the cone, a complete analysis was not made. In the adult, however, both the hyperstome and hypostome possess several heavily sclerotized strengthening regions on their lateral surfaces. The distal end of the cone is membranous, very flexible, and finely setuliferous.

Postantennal Process

The postantennal process is discussed after the mandible because of the possibility that it is a true appendage (Heegaard, 1947:59, 203–206). The terminology used, with regard to the author's present beliefs, is the same as that used in Lewis (in press). The fact that, in *L. dissimulatus,* this process does not appear until the third chalimus, long after all of the other oral appendages are present, is an indication that it is not a true appendage, although Heegaard (1947:205) presents a hypothesis for its late appearance. The arguments both for and against the term "appendage" being applied are, however, strong enough so that this author prefers not to commit himself until further studies can be made.

The postantennal process of the third chalimus (Fig. 16*m*) is a blunt-tipped, spinelike process projecting posteriorly from an indistinct plate on the ventral surface of the cephalothorax posterior and lateral to the base of the second antenna. The proximal end of the process bears two minute nodules, each with one setule.

The postantennal process of the fourth chalimus (Fig. 16*n*) is more strongly developed and sharply pointed than that of the preceding stage. The indistinct plate still bears the process, from the base of which arise two minute nodules as in the preceding stage, each with a single setule.

The postantennal process of the female and male fifth chalimus (Fig. 16*o*) is more strongly developed than in the preceding stage; the process has become distinctly curved medially and, in addition to the two single setule-bearing nodules on the proximal end, now has a third nodule just medial to the distal region of the process. The plate from which the process of the preceding two stages arose is now almost completely invisible.

The postantennal process of the female and male sixth chalimus (Fig. 16*p*) is curved medially as in the preceding stage. The proximal region is, however, more developed, the inner margin irregular, not evenly curved as in previous stages. Two nodules are present on the proximal end but, in contrast to the last three stages, each now bears two fine setules. Only one setule was visible on the third nodule, although the extremely small diameter and short length of the setules made observation difficult and the number may be incorrect. The plate from which the process arises is more distinct than in the preceding stage.

The adult female and male postantennal process (Fig. 16*q*) is similar to that of the sixth chalimus, although the distal end is more sharply curved. The proximal nodule of the two nodules on the base of the process now gives rise to three setules, the distal nodule to four. The third nodule of the chalimus stages did not appear to be present.

Postoral Process

The postoral process is of the same general make-up as the postantennal process, although it is first present on the copepodite instead of the third chalimus. The process has been called the first maxilla and the second maxilla. Its structure, in addition to the location of the origin of the subesophageal ganglionic nerve that innervates it (adjacent to nerves that go to the lateral musculature and the postantennal process) and the inability to determine its anlage, has caused the author to use the term "postoral process."

The postoral process of the copepodite (Fig. 16*r*) consists of a posteriorly projecting, well-developed, distally pointed process and two setule-like projections just medial to the proximal end of the process. Both the process and the projections arise just lateral and slightly posterior to the base of the mouth cone. The inner margin of the process is convex, the outer concave with a slight proximal swelling. A minute, heavily sclerotized, lobelike structure is present just lateral to the process and appears to be con-

nected to the same poorly defined plate from which it arises.

The postoral process of the first chalimus (Fig. 16*s*) is distinctly different from that of the copepodite. The process consists of a two-parted, spinelike process and a setule-bearing nodule, both attached to a well-defined plate just lateral and posterior to the base of the mouth cone and contiguous with the plate present at the base of the cone. The two-parted, spinelike process projects posteriorly; both parts are rounded distally, the second part being attached to the distal end of the first. The greatest length of the second part is approximately two-thirds that of the first. The setule-bearing nodule is just anterior to the base of the spinelike process, at the anterior end of the plate. The nodule is small and gives rise to two slender setules from its distal surface.

A general transition is apparent from the first chalimus to the adult. The two-parted condition of the postoral process is still evident in the second chalimus (Fig. 16*t*), but in the third (Fig. 16*u*) the two parts become fused, the distal portion becomes more sharply pointed, and the base spreads out to its greatest width, in the adult (Fig. 16*y*), the width in the adult being just slightly less than the length. The plate from which the process and the setule-bearing nodule arise becomes indistinct in the second chalimus, third chalimus, and fourth chalimus, then becomes more distinct in the fifth chalimus but appears as two parts. These two parts of the plate are evident in the sixth chalimus and in the adult. The anterior plate has a posteriorly directed lobe (within, not projecting from, the cephalothorax) just medial to which the setule-bearing node projects. The posterior plate forms the base of the spinelike process and is continuous with it. The setule-bearing node enlarges somewhat throughout development and adds another setule to its armature, having two slender setules in the second chalimus, three in the third and fourth chalimus, two (?) in the fifth, and three in the sixth chalimus and in the adult. All the setules are borne on the distal surface of the nodule.

Maxilla

The term "maxilla" is applied to the pair of oral appendages immediately behind the mouth cone and postoral processes. This appendage pair has gone under a variety of names because of the terminology applied to the postantennal and postoral processes. Inasmuch as the term "process" is here applied to the postantennal and postoral structures, the first pair of recognizable appendages behind the mouth are designated as the maxillae.

The maxilla is first present in the copepodite (Fig. 17*a*) and is found attached to the ventral surface of the cephalothorax just posterior and lateral to the postoral process. The first segment of the two-segmented structure is strongly developed; the proximal surface possesses a medial projection that articulates with the cuticle of the body at the point of attachment of the appendage. The distal margin of the first segment is flat; the surface is depressed and receives the proximal surface of the second segment. The second segment is elongate, being slightly longer than the first segment and much thinner. The lateral margins of the second segment are irregular, the outer proximal margin curving inward to the irregular proximal surface, the inner margin with several flatly convex swellings. The distal region of the second segment is slightly swollen, the distal margin broadly rounded. Two processes are present on the distal region and extend out from the segment. The outer process is spinelike and is less than one-fourth the length of the segment; this process possesses a series of minute, tine-like projections along the inner margin giving it a brushlike appearance. The inner process arises from the posterior lateral surface of the distal region, not the distal surface as does the outer process; it is lobate and flimsy in nature, its length approximately equal to that of the outer process.

The segments of the maxilla of the first chalimus (Fig. 17*b*) are similar in general make-up to those of the copepodite. The proximal articulation surface of the copepodite appendage is, however, absent in the first chalimus and, further, the first segment is somewhat thicker. The distal surface of the first segment is concave and forms the articulation surface for the ball-shaped proximal end of the second segment. The inner of the two terminal processes on the second segment is slightly longer than the outer and is tapered to a sharp point. The outer of the two processes is simple and lobate, lacking

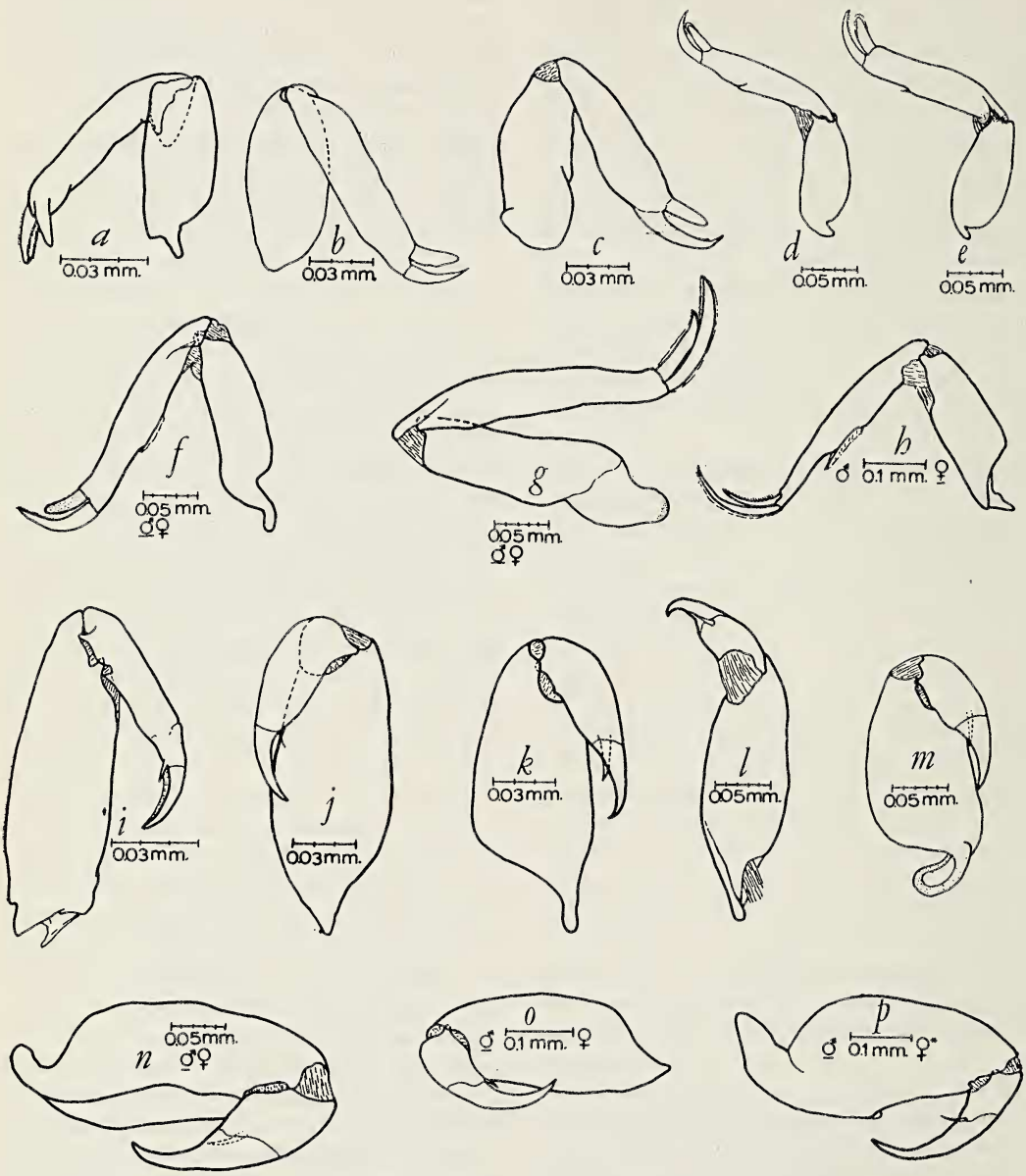

FIG. 17. Maxillae and maxillipeds of developmental stages of *L. dissimulatus*. *a–h*, Maxillae: *a*, Copepodite; *b*, first chalimus; *c*, second chalimus; *d*, third chalimus; *e*, fourth chalimus; *f*, fifth chalimus; *g*, sixth chalimus; *h*, adult. *i–p*, Maxillipeds: *i*, Copepodite; *j*, first chalimus; *k*, second chalimus; *l*, third chalimus; *m*, fourth chalimus; *n*, fifth chalimus; *o*, sixth chalimus; *p*, adult. For minor differences between male and female adult maxilliped, see description of appendage.

the series of tine-like projections of the copepodite process. The arrangement of the terminal processes thus appears to be reversing itself and, as will be described for later stages, does reverse so that the inner process is complex and the outer simple.

The second chalimus maxilla (Fig. 17*c*) appears to have degenerated slightly from that of the preceding stage. The shape varies somewhat in different specimens and, in general, appears to be of a rather plastic nature. The first and second segments are of approximately equal length, the first appearing more strongly developed than the second. The outer proximal corner of the first segment is heavily sclerotized and appears to function as an articulation surface. The distal end of the first segment is slightly narrower than the proximal, and the lateral margins are somewhat irregular; the distal region is heavily sclerotized on the inner portion although no distinct articulation surfaces are visible. The second segment is narrower proximally than distally, the segment appearing almost club-shaped. The proximal margin of the segment is almost included in the inner lateral margin, both lateral margins are somewhat wavy, and the distal margin is rounded. The inner terminal process is relatively longer than in the preceding stage, now being approximately twice the length of the outer process; further, the process is tapered to a sharp point and possesses several minute setules on the distal end of the outer margin. The inner terminal process is simple and lobate, almost identical to that of the first chalimus.

The maxilla of the third chalimus (Fig. 17*d*) differs somewhat from that of the second chalimus. The first segment is approximately two-thirds the length of the second, its proximal end projecting as a curved, lobate process that serves as an articulation surface. The outer lateral margin is broadly convex, the inner flatly convex; the greatest width is slightly less than one-half of the greatest length and the general shape of both of the segments appears to be more distinct than in the preceding stage. The distal margin of the first segment is irregular and heavily sclerotized, the irregularities serving as articulation surfaces for the proximal end of the second segment. The second segment is slender, and the inner and outer margins are generally flatly convex. The proximal margin of the second segment is now completely included in the inner margin. The proximal surface possesses two small knoblike projections with a concave surface between them; both of the projections and the concave surface articulate with reciprocal processes on the irregular distal end of the first segment. The middle of the inner margin of the second segment now has a short groove extending from the surface inward and proximally; this groove corresponds to the position of one of the spines present on the adult appendage. The distal end of the segment is tapered to a medial point and possesses the two terminal processes present on preceding maxilla-bearing stages. The inner of the two processes now curves sharply outward, over the distal end of the outer process, and is minutely frilled along its outer distal margin. The outer process is lobate, approximately two-thirds the length of the inner process; the distal margin bears a fine membrane.

The maxilla of the fourth chalimus (Fig. 17*e*) still bears the somewhat degenerate appearance of the third chalimus appendage. Except for the distal end, the first segment is similar to that of the preceding stage. The outer distal margin of the segment is concave; the distal end of the inner lateral margin is also concave, forming a knoblike projection at the junction of the two which is heavily sclerotized. The proximal surface of the second segment, included in the inner lateral surface, is bilobed. The bilobed condition of the surface appears to be due to a split or division occurring in the small concavity separating the two heavily sclerotized knobs of the previous stage. The separation between the two lobes forms an articulation surface for the knoblike projection of the inner distal surface of the first segment and the lobes themselves articulate in the concavities on the distal and inner distal lateral surfaces of the first segment. The middle of the inner lateral margin of the segment is indented in the region of the groove of the preceding stage and bears a single spinule. The second segment is tapered slightly from the indentation to the distal end, which is tipped by the two terminal processes. The inner terminal process is similar to that of the preceding stage, the outer process is slightly longer, and the fine membrane now extends

around the distal end and distal lateral margins.

Both segments of the maxilla of the fifth chalimus female and male (Fig. 17*f*) are more slender and appear more elongate than those of the preceding stage. The first segment is slightly shorter than the second and its proximal end projects as an irregular, lobate articulation process. The outer margin of the segment is flatly convex; the inner is slightly convex proximally, flat medially and concave distally. The outer distal margin is tapered abruptly to a knoblike projection of the inner distal surface that appears to be the enlarged projection of the distal end of the first segment of the fourth chalimus. The second segment is slender, the proximal end two-parted and included in the inner lateral margin. The junction of the two parts of the proximal end forms a concave surface that articulates on the knoblike process on the distal end of the first segment. The outer lateral margin of the second segment is generally flatly convex; the inner lateral margin is slightly irregular, with a slight indentation in the middle that bears a single spinule and a fine membrane connected to the spinule and extending proximally for a short distance. The distal end of the second segment is almost flat and bears two terminal processes. The inner terminal process is relatively longer than in the preceding stage, being 1½ times the length of the outer process; the outer margin is fringed with a fine, lightly frilled membrane. The outer process is lobate and covered with minute, hairlike projections.

The maxilla of the female and male sixth chalimus (Fig. 17*g*) is similar to that of the fifth chalimus in general shape. The segments, and especially the proximal projection of the first segment, are heavier; the knoblike projection of the inner distal surface is on the inner corner so that it forms the junction of the inner lateral and inner distal surfaces. The proximal end of the second segment, included in the inner lateral surface, again appears two-lobed, the proximal lobe extending proximally and forming the point of attachment for the muscle that abducts the second segment. The distalmost of the two lobes forms an indentation in the margin that extends for a short distance although there is a continuation, as a distinct line of division between the two lobes, running almost parallel to the lateral margins of the segment. The middle of the lateral surface of the second segment is tapered slightly but abruptly; the spinules and membrane present in this region in the adult and in the preceding stage were not present on any of the specimens examined. The two terminal processes on the flat distal end of the second segment are both slightly larger than in the preceding stage; the outer is now pointed distally and both have a fine, membranous margin along their inner and outer surfaces.

The maxilla of the adult female and male (Fig. 17*h*) is more definitely shaped than any of the preceding stages and the first segment more strongly developed than in the preceding two chalimus stages. The first segment is short and stocky, the inner proximal end protruding as an irregular articulation surface. The distal lateral margins of the first segment are tapered irregularly to the somewhat narrow distal surface, the median portion of which projects as a narrow, lobate articulation surface that is heavily sclerotized. The second segment is elongate, the lateral margins irregularly convex. The proximal surface, included in the inner lateral surface, is irregular, with a slight concavity that forms the place of articulation for the medial projection of the distal surface of the first segment. The middle of the inner margin is notched in two places, the proximal notch bears a minute spine not present in any preceding stage, and the distal notch bears a larger spine, about twice the length of the proximal spine. A fine membrane is also present and connects the two spines. The two terminal processes arising from the step-shaped distal end of the second segment are more elongate than those of the preceding stage. The innermost of the two processes is about 1½ times the length of the outer and possesses a membrane along the outer margin. The outer process is fringed by a frilled membrane along the outer margin.

Maxilliped

The maxillipeds have been termed the first thoracic appendages in copepods as well as in other crustaceans and the maxillae as the last cephalic appendages (Borradaile et al., 1958: 347–348). This terminology is accepted by most authors, including those who apply the term "first maxilla" to the postoral process, but is not accepted by those workers who call the post-

antennal process the first maxilla and the postoral process the second maxilla. In this latter case the first pair of identifiable appendages behind the mouth thus become the first maxillipeds and the last pair of appendages before the thoracic legs become the second maxillipeds. With the use of the term "maxilla" for the first pair of identifiable appendages behind the mouth, the term "maxilliped" is here applied to the pair of appendages anterior to the first thoracic legs.

The maxillipeds are first present in the copepodite (Fig. 17*i*) as uniramous, two-segmented appendages attached to the ventral surface of the cephalothorax posterior and slightly medial to the base of the maxillae. The first segment is slightly less than twice the length of the second; its proximal end is broad and has a poorly developed articulation surface that projects from the middle of the surface. The lateral margins of the first segment are slightly curved, the anterior margin flatly concave, the posterior flatly convex; the distal anterior margin is tapered sharply inward to the narrow distal end. Both the distal and inner distal lateral surfaces have several rather heavily sclerotized projections and depressions, each fitting depressions or receiving projections from the proximal surface of the second segment. The second segment is slender, the inner margin shorter than the outer although both are slightly irregular. The distal region of the second segment is tapered to the short distal surface which bears a strongly developed, spinelike terminal process that curves medially evenly. A slender, short, spinelike structure is present as an accessory process and arises from the inner distal surface of the segment. The division between the segment and the terminal process is distinct and complete, that between the segment and accessory process indistinct and incomplete; the terminal process bears a membranous fringe along the inner margin.

The first chalimus maxilliped (Fig. 17*j*) is more strongly developed than in the copepodite. The first segment is approximately the same length, with regard to the second segment, although appearing heavier, its width being slightly greater than one-third of its length. The inner proximal surface of the first segment projects as a tapered articulation process, and the lateral margins of the segment are flatly convex, the outer margin longer than the inner; the distal surface is angled inward and downward and possesses two distinct, heavily sclerotized articulation surfaces for the second segment. The second segment, including the terminal process, is tapered from the broad proximal to pointed distal end. The proximal region of the segment has two lobate projections, one from the anterior surface and the second from the posterior, which articulate with the indentations of the distal surface of the first segment. A small setalike accessory process arises from the inner surface of the segment, at the distinct junction of the segment and the terminal process. The terminal process is heavily sclerotized, curves inward, and lacks the marginal membrane of the previous stage.

The changes that occur in the maxilliped from the first chalimus to the adult (Fig. 17*k–p*) are relatively minor. The general shape remains the same and the armature of the second segment does not change. The articulation surface that projects from the proximal region changes slightly, becoming somewhat longer in the second chalimus (Fig. 17*k*) and then gradually curving in the third chalimus (Fig. 17*l*) and fourth chalimus (Fig. 17*m*) until it becomes almost recurved in this and the fifth chalimus stages. The articulation projection then becomes lobate in the sixth chalimus (not visible in Fig. 17*o*) and the adult (Fig. 17*p*). The inner surface becomes grooved in the fifth chalimus and remains that way up to and including the adult. The division between the second segment and terminal process becomes rather indistinct in later stages of development. The adult male maxilliped has a small shelflike structure that is present on the middle of the inner margin of the first segment. This structure appears in the last moult, from the sixth chalimus to the adult, and is the only apparent difference between the maxilliped of the female and the male.

Sternal Furca

The sternal furca is a single process between and slightly posterior to the maxilliped bases and is another structure about which little is known. Most authors have simply reported its presence or absence and utilized this as a taxonomic characteristic. The position of the structure, posterior to the maxilliped bases, does not

allow any specific interpretation as to its origin. If the maxillipeds are the first pair of thoracic appendages, the sternal furca may be the remnant of the sternal plate which exists between the first three pairs of thoracic legs of *L. dissimulatus* and many other caligoids. No definitive evidence for this idea can be offered, however, other than the relative position to the maxillipeds and the presence of sternal plates on some of the thoracic legs. Futhermore, the sternal furca in *L. dissimulatus* does not appear until the fourth chalimus, long after the maxillipeds, the thoracic legs, and the sternal plates of the first two thoracic legs. The hypothesis has, therefore, at least one pitfall unless, and no information is given to support this, a shift can

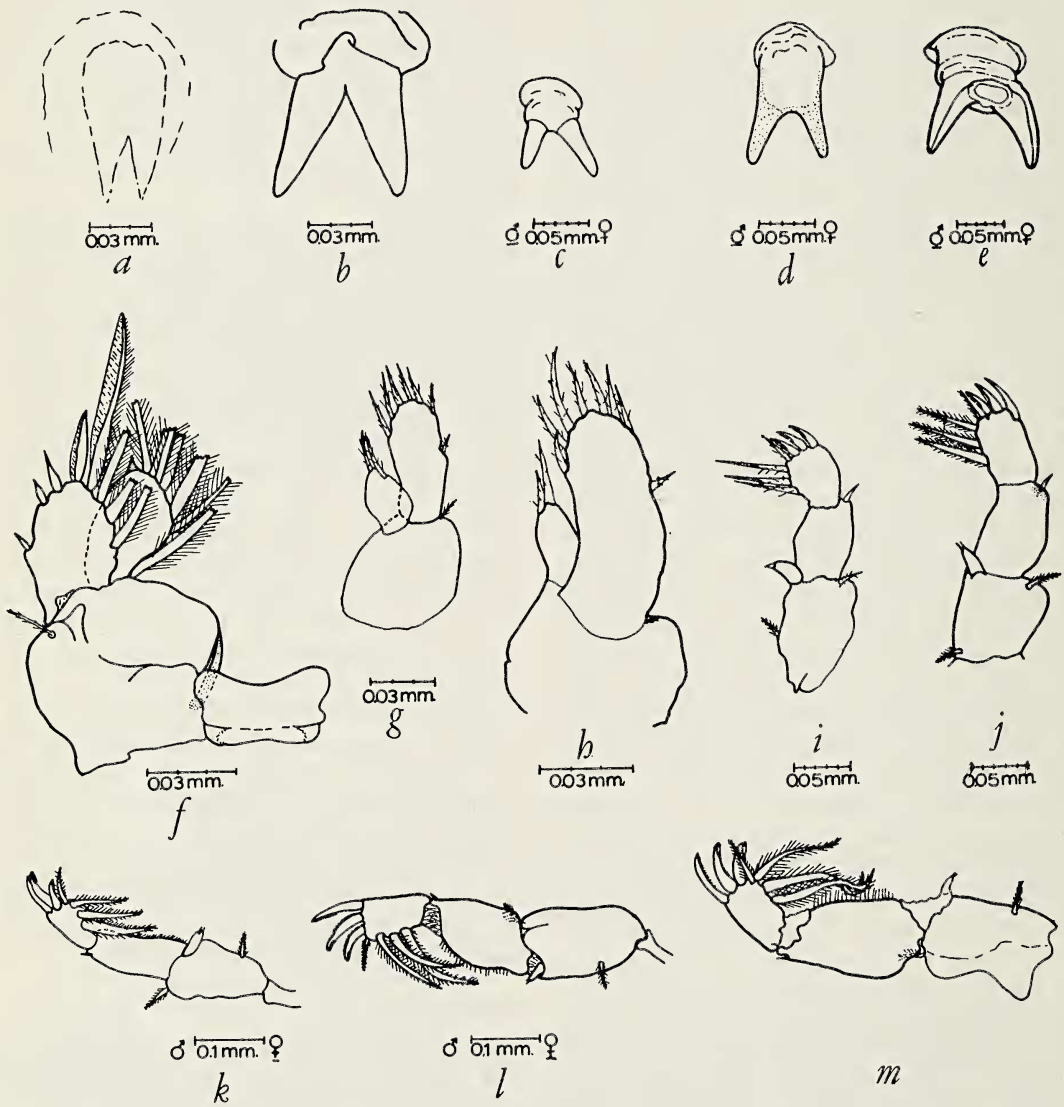

FIG. 18. Sternal furcae and first thoracic legs of developmental stages of *L. dissimulatus*. *a–e*, Sternal furcae: *a*, Third chalimus; *b*, fourth chalimus; *c*, fifth chalimus; *d*, sixth chalimus; *e*, adult. *f–m*, First thoracic legs: *f*, Copepodite; *g*, first chalimus; *h*, second chalimus; *i*, third chalimus; *j*, fourth chalimus; *k*, fifth chalimus; *l*, sixth chalimus; *m*, adult.

occur in the time that a structure appears in development. If this were possible, then the status of the postantennal process must also be reviewed. The presence of a short but distinct muscle that is attached to the sternal furca and the mobility of the process exhibited by adult specimens make it difficult to accept Heegaard's suggestion (1947:77–78) that the sternal furca is a cuticular spine.

The sternal furca of the fourth chalimus is visible developing underneath the third chalimus cuticle (Fig. 18*a*). The process is indistinctly visible between and slightly posterior to the bases of the maxillipeds but does not project from the ventral surface. The proximal end is broadly rounded, the bifurcation extends less than one-half of the total length of the process, and the tines are sharply pointed.

After the moult into the fourth chalimus, the sternal furca (Fig. 18*b*) is distinct, projecting from the ventral surface of the cephalothorax. The greatest width of the process is approximately two-thirds of the greatest length. The bifurcation extends slightly more than two-thirds of the length of the process. The tines are angled outward slightly and are bluntly rounded distally.

The sternal furca of the fifth chalimus (Fig. 18*c*) is well developed. The bifurcation of the process extends about one-half the length of the process. The tines appear distinct, separated from the base of the process by a groove; they are also angled outwards slightly and are bluntly pointed.

The tines of the sternal furca of the sixth chalimus do not appear distinct from the base as in the preceding stage. The bifurcation extends slightly more than one-half the length of the process; the tines are angled outward slightly and are bluntly pointed.

The sternal furca of the adult male and female (Fig. 18*e*) is more heavily developed than in the preceding stages. The tines have a flat inner surface in contrast to the round inner surface of the previous stages but are still angled outwards slightly and have a blunt tip.

Thoracic Leg I

The armature and character of the membranes, spines, and setae comprising the armature, are given in Table 2.

The first thoracic leg is present in the copepodite. The appendage (Fig. 18*f*) is biramous; the protopodite, exopodite, and endopodite are each one-segmented. The protopodite is wider distally than proximally, its greatest width slightly more than the greatest length; a single lightly plumose seta is present just lateral to the base of the exopodite and an indistinct, seta-like process is present on the proximal inner margin. The exopodite is palm-shaped, its lateral and distal margins continuous. The outer margin of the exopodite segment bears four spines, the proximal three of which are simple, the fourth with a membrane along the outer margin. The endopodite is also palm-shaped, the lateral and distal margins again continuous. The outer distal surface bears a small, triangular, spinelike projection in addition to the setae shown in Table 2.

The distinct shape of the copepodite first thoracic leg is lost in the moult from the copepodite into the first chalimus. The first thoracic leg of the first chalimus (Fig. 18*g*) appears flabby, the armature seems to have degenerated, and the long plumose setae borne by the exopodite and endopodite of the copepodite first leg, and presumably used in swimming, are lost and replaced by short, lightly plumose setae. The protopodite is one-segmented, its width and length about equal; the distal end is somewhat narrower than the proximal although this is variable in different specimens. A single lightly plumose seta is present on the distal lateral surface just lateral to the base of the exopodite, and the seta-like process of the preceding stage is absent. The exopodite is one-segmented and dactyliform, the proximal end is wider distally than proximally, and the greatest length is approximately 2½ times the greatest width. The lateral margins of the segment are slightly irregular, the distal margin broadly curved. A lightly plumose seta is present on the middle of the outer lateral surface and six lightly plumose setae are present on the distal end. The spines present on the exopodite segment of the copepodite appendage are completely absent in the first chalimus. The endopodite is one-segmented and irregularly lobate, its length slightly less than two-thirds that of the exopodite. The endopodite bears two lightly plumose setae on its distal surface.

Two distinct trends can be noticed in the

TABLE 2

ARMATURE OF FIRST THORACIC LEGS OF DEVELOPMENTAL STAGES*

STAGE	MARGIN	PROTOPODITE	EXOPODITE 1	EXOPODITE 2	ENDOPODITE
Copepodite	outer	1s	3h,1Hm		
	inner	1P′	3P,1Q		7P
Chalimus I	outer	1p	1p,3P		1P
	inner		3P		1P
Chalimus II	outer	1p	1P,3P		1P
	inner		4P		1P
Chalimus III	outer	1p	1rh	3H	1rh?
	inner	1p		3P,1P	?
Chalimus IV	outer	1p	1rh	3H	1rh?
	inner	1p		3P,1P	1rh?
Chalimus V	outer	1p	1rh	3H	1rh?
	inner	1p	c	3P,1P	1rh?
Chalimus VI	outer	1p	1rh	3H	1rh?
	inner	1p	c	3P,1P	1rh?
Adult	outer	1p	1rh	3H,1P	?
	inner	1p	c	3P	?

* For explanation of symbols see Fig. 1.

gradual change of the first thoracic leg from the first chalimus stage to the adult. There is a gradual reduction in the size of the endopodite, with regard to the exopodite. Both the exopodite and the endopodite are of approximately equal size in the copepodite but even in the first chalimus the endopodite is distinctly smaller than the exopodite, a change that is carried through later development until in the adult the endopodite is a mere rudiment, vastly smaller than the exopodite. The second trend is the gradual elongation of the exopodite segment from the palm-shaped copepodite segment to the elongate second chalimus segment (Fig. 18*h*), then the division of this segment into two segments in the third chalimus (Fig. 18*i*) and the later elongation of each of the two segments, especially the proximal, to the adult condition (Fig. 18*m*).

The armature of the first thoracic leg changes in character more than in quantity from the first chalimus to the adult. The second chalimus exopodite bears seven lightly plumose setae on the distal surface and one short, lightly plumose seta from the middle of the outer lateral surface. The exopodite of the third chalimus, a two-segmented structure, bears three spines and one lightly plumose seta on the distal surface and three lightly plumose setae on the inner lateral surface of the second or distalmost segment in addition to a single, spinelike process on the outer distal lateral corner of the first segment. The total number of processes on both of the segments is the same as the number on the single exopodite segment of the second chalimus although the character is quite different. The armature of the exopodite remains the same as that of the third chalimus throughout development except for the addition of a row of setules along the inner surface of the first segment. The two lightly plumose setules on the distal surface of the endopodite segment of the first chalimus are found through most of the development (see Table 2) although distinctly reduced in size until in the adult they appear as minute, indistinct projections from the distal surface of the rudimentary endopodite. One other change occurs in the armature of the first thoracic leg, the addition of a small, lightly plumose setule on the proximal inner margin of the protopodite segment of the third chalimus.

Some change occurs in the shape of the first thoracic leg segments but these are of a rather minor nature and are shown in Figure 18*f–m*.

Thoracic Leg II

The armature and character of the membranes, spines, and setae comprising the armature are given in Table 3.

The second thoracic leg is first present in the copepodite stage. As with the first thoracic leg, the appendage appears to degenerate in the first few chalimus stages and then gradually takes on the appearance of the adult appendage in the late chalimus.

The second thoracic leg of the copepodite (Fig. 19*a*), as in all of the remaining stages, is biramous. The protopodite is one-segmented, the width of the proximal and distal ends being about equal and the greatest length about three-fourths of the width. The lateral margins of the segment are broadly convex, and the distal margin is irregular. A single lightly plumose seta is present on the protopodite just lateral to the exopodite base. The exopodite is one-segmented and ovoid, and the distal margin is distinct from the outer lateral margin but is continuous with the inner. The proximal end of the exopodite is minutely bilobed and heavily sclerotized, forming an articulation surface that is contiguous with irregularities on the lateral distal surface of the protopodite. The outer surface of the exopodite bears three spines, the proximal two of which are simple, the distal long and fringed by a membrane along its outer margin. The endopodite is one-segmented, the proximal end narrow and the distal end broad; the distal two-thirds of the segment is bent inwards. The lateral and distal margins of the segment are both distinct. Both the exopodite and endopodite bear several plumose setae as indicated in Table 3.

The second thoracic leg of the first chalimus (Fig. 19*b*) is much more simple than the copepodite appendage. The protopodite is one-segmented, and its greatest length is approximately two-thirds of its greatest width. Both of the lateral margins are continuous with the distal margin although the entire outline of the segment is somewhat irregular. The single seta present on the copepodite protopodite is absent in this stage. The exopodite and endopodite are of approximately equal length and both are dactyliform. The exopodite is approximately one-half as wide as long although slightly wider distally than proximally; the lateral margins are wavy, the distal broadly rounded. A single naked seta is present on the middle of the outer lateral surface and five lightly plumose setae on the distal surface. The endopodite is irregularly rounded distally; the lateral and distal margins are con-

TABLE 3

ARMATURE OF SECOND THORACIC LEGS OF DEVELOPMENTAL STAGES*

STAGE	MARGIN	STERNAL PLATE	PROTOPODITE 1	PROTOPODITE 2	EXOPODITE 1	EXOPODITE 2	EXOPODITE 3	ENDOPODITE 1	ENDOPODITE 2	ENDOPODITE 3
Copepodite	outer		1p		2h,1Hm					
	inner				3P,1Q			6P		
Chalimus I	outer				1p',3P			2P		
	inner				2P			2P		
Chalimus II	outer				2P,2P			2P		
	inner				4P			1P,3P		
Chalimus III	outer			1p	f,1H	4H,3P		c	c,2P	
	inner		1P	f,1s	c	c,2P		1P	4P	
Chalimus IV	outer			1p	f,1H	3H,1Q,2P			2P,2P	
		f								
	inner		1P	f,1s	c,1P	c,3P		1P	3P	
Chalimus V	outer			1p	f,1H	3H,1Q,2P		c,C	c,1P,3P	
		f								
	inner		1P	f,1s	c,1P	c,3P		1P	c,3P,2P	
Chalimus VI	outer		1s	1p	f,1H	1H	2H,1Q,3P	c,C	c	c,3P
		f								
	inner		1P	f,1s	c,1P	c,1P	c,2P	1P	c,2P	3P
Adult	outer			f,1p	f,1H	1H	2H,1Q,2P	c,C	c	c,3P
		f								
	inner		1s,1P	f,1s	c,1P	c,1P	c,3P	1P	c,2P	c,3P

* For explanation of symbols see Fig. 1.

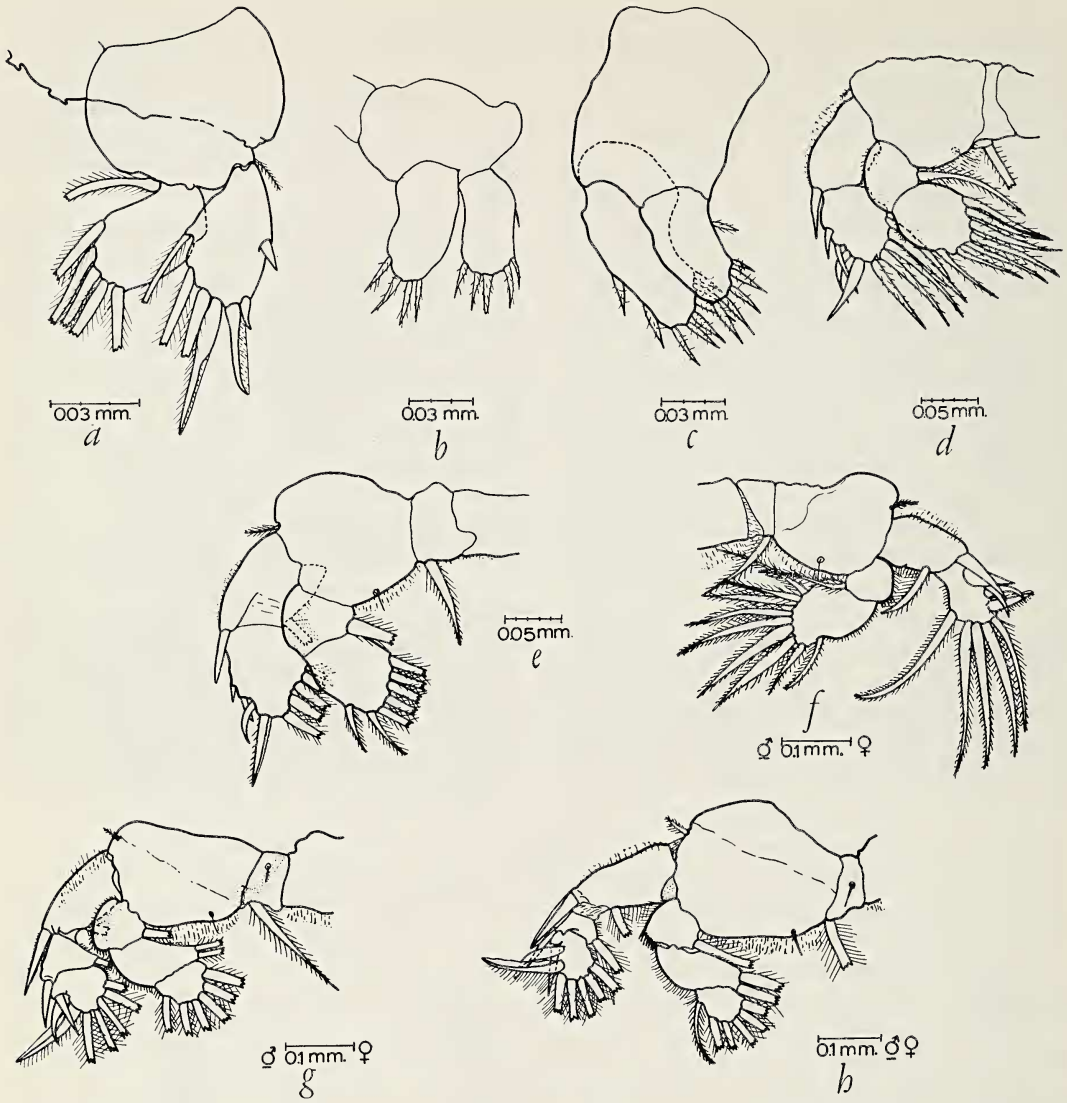

FIG. 19. Second thoracic legs of developmental stages of *L. dissimulatus*. *a*, Copepodite; *b*, first chalimus; *c*, second chalimus; *d*, third chalimus; *e*, fourth chalimus; *f*, fifth chalimus; *g*, sixth chalimus; *h*, adult.

tinuous. The greatest width of the endopodite segment is approximately one-half of the greatest length; the distal surface bears four lightly plumose setae.

Some enlargement has occurred in the second thoracic leg of the second chalimus (Fig. 19*c*), especially in the protopodite. The protopodite is still one-segmented, its greatest width being approximately three-fourths of its greatest length. The proximal margin of the segment is indistinct, and the lateral margins are almost parallel. The protopodite is approximately twice the length of the first chalimus protopodite although its width is about the same. The one-segmented, dactyliform exopodite is attached to the distal surface of the protopodite. The greatest width of the segment is approximately one-half of the greatest length; the lateral margins are irregular, the distal rounded. Two lightly plumose setae are present on the distal one-half

of the outer surface and six are borne on the distal surface. The one-segmented, dactyliform endopodite is attached to the inner distal surface of the protopodite. The greatest length of the segment is about two-thirds of the length of the exopodite, its width about one-half of its length. The endopodite is tapered slightly towards the rounded distal end which bears five lightly plumose setae; an additional lightly plumose seta is present on the middle of the inner margin.

As with the first thoracic leg, the second shows a rather distinct transition in the moult from the second chalimus to the third. The appendage in the third chalimus (Fig. 19*d*) has changed from the rather generalized condition in the second chalimus to a condition which, with some exceptions, resembles that of the adult.

The protopodite of the second thoracic leg of the third chalimus is two-segmented. The first segment is narrow and forms a strip between the sternal plate and the second segment. A single plumose seta arises from the inner surface of the first segment. The second segment is broad and flattened, its greatest width is almost three-fourths of the greatest length, the outer margin is irregular, and the inner margin is convex. The exopodite, which is attached to the outer distal surface, is two-segmented. The length of the first segment is slightly greater than that of the second, and the greatest width is approximately two-thirds of the length; the lateral margins are irregularly convex. A long spine is present on the outer distal surface and is directed distally; the length of the spine is slightly less than two-thirds of the segment length. The second segment is slightly longer than wide, and the proximal end is narrower than the distal; both of the lateral margins and the distal margin are distinct, not continuous, and are irregular; the outer lateral surface bears four spines on the distal one-half of the segment. The proximalmost of the four spines is short and directed distally and laterally; the second spine is directed in the same manner as the first but is considerably longer; the third is directed laterally, curves distally, and is about the same length as the second; the fourth or distalmost spine is directed laterally and is more strongly developed than the preceding three. The endopodite, attached to the inner distal surface of the protopodite, is also two-segmented. The first segment is approximately two-thirds as wide as long and is curved inwards, the outer lateral margin being much longer than the inner and convexly curved. The second segment is slightly less than 1½ times the length of the first and is longer than wide; both of the lateral margins are flatly convex and distinct from the distal margin, which is irregularly rounded. Both the exopodite and the endopodite bear setae, as indicated in Table 3.

The second thoracic leg of the fourth chalimus (Fig. 19*e*) is similar to that of the third chalimus. There has been some expansion of the protopodite segments and the first exopodite segment. The setae appear to be more plumose and, in general, the armature is more like that of the adult.

The second thoracic leg of the fifth chalimus (Fig. 19*f*) is similar to that of the preceding stage although changes have occurred in the shape and the armature. The protopodite is two-segmented, the first segment short, being approximately one-third the length of the second segment; the width of the first segment is approximately three-fourths of the length. The outer margin of the first protopodite segment is longer than the inner, the proximal margin is angled, and the distal is straight. Further, the outer proximal surface of the segment has a small knoblike projection that articulates in a C-shaped depression in the end of the sternal plate (not shown in the figure), and the inner margin bears a single plumose seta. The second segment is swollen distally, the greatest width of the distal region being approximately four-fifths of the greatest length; the outer lateral margin of the segment is irregular, the inner broadly convex. The exopodite is still two-segmented, the first segment slightly longer than the second. The outer margin of the first segment is convex, and the inner margin is slightly irregular. The outer distal corner of the first segment bears a long, distally projecting spine that extends to the distal region of the second segment. The second segment is palm-shaped, being wider distally than proximally. The greatest width of the segment is approximately two-thirds of the greatest length; the outer lateral margin is irregular and bears three strongly-

developed spines, the proximal two extending distally and laterally, the distalmost extending laterally and curving distally. The simple fourth spine of the third chalimus bore a membrane on the inner margin and a row of setules on the outer in the fourth chalimus; this condition is reversed in the fifth chalimus. The endopodite is two-segmented; the first segment is short, its width slightly greater than the length which is approximately one-half that of the second segment. Both of the lateral margins of the first segment are convex, the outer twice the length of the inner. The second segment is irregularly palm-shaped, and the lateral margins are irregular although distinct from the distal margin; the greatest width of the segment is approximately two-thirds of the greatest length.

The second thoracic leg of the sixth chalimus (Fig. 19*g*) is basically the same as that of the adult. The protopodite is two-segmented; the first segment is short, less than one-third of the length of the second. The second segment is broader distally than proximally, its greatest width approximately two-thirds of the length. The lateral margins of the second segment are slightly wavy, the inner generally convex. The exopodite is now three-segmented, the division occurring in the second segment of the previous stage, just distal to the proximalmost spine. The first exopodite segment is slightly longer than the combined lengths of the succeeding two segments, and its lateral margins are flatly convex. The single spine is slightly denticulated and strongly developed and extends past the distal end of the second segment. The second segment is short, flared from the narrow proximal to broad, concave distal surface. A single simple, although well-developed, spine is present on the outer distal surface. The third segment is short, its length approximately equal to that of the second segment. The distal one-half of the segment is broadly rounded and a small, steplike indentation is present in the proximal one-half of the outer margin. A well-developed, simple, distally projecting spine is present in the indentation and a second well-developed, simple spine projects laterally and curves distally from the outer lateral surface at the junction of the curved and indented margins. The endopodite is also three-segmented. The first segment is approximately equal in length to the second; the outer margin is broadly rounded and approximately 4 times the length of the short, irregular inner margin. The second segment is flared from the narrow proximal to broad distal end, as in the second segment of the exopodite. The outer margin of the second segment is flatly convex, the inner slightly concave. The third segment is short, being approximately three-fourths of the length of the second segment. The distal and lateral surfaces are irregularly rounded, the margins continuous.

With the exception of some minor changes in the shape and armature of the segments, the description of the second thoracic leg of the sixth chalimus can be applied to the adult appendage (Fig. 19*h*).

Thoracic Leg III

The armature and character of the membranes, spines, and setae comprising the armature are given in Table 4.

The biramous third thoracic leg is first present as a recognizable appendage in the first chalimus (Fig. 20*a*). As mentioned earlier, however, two spinelike processes are present on the third pedigerous segment of the copepodite and may represent the third legs in this stage of development. The protopodite of the third thoracic leg of the first chalimus is one-segmented, its greatest width and length about equal. The somewhat irregular outer lateral margin is more than twice the length of the inner and two naked setules are present on the outer lateral surface just lateral to the exopodite base. The exopodite is one-segmented, broader than long; its lateral margins are generally convex and the distal margin is flat although variable in shape in different specimens. Four spinule-like processes project from the distal region of the exopodite. The endopodite is also one-segmented and broadly rounded, both of the lateral and the distal margins being continuous; the greatest width of the segment is slightly more than the length.

The protopodite of the third thoracic leg of the second chalimus (Fig. 20*b*) is much larger than that of the preceding stage, most of the increase in size being due to the increase in the lateral surface. The irregular proximal end of the one-segmented protopodite is broad, approximately twice the width of the distal end. The outer lateral margin is almost 4 times the

length of the inner. The exopodite and the endopodite differ from those of the preceding stage in shape and armature. The one-segmented exopodite is broader than long, the lateral margins are irregular although slightly convex, and the distal margin is irregularly rounded. Both the outer and inner lateral margins have several irregularly spaced setules and the distal surface bears two spinelike processes. The one-segmented endopodite is about one-half the length of the exopodite although both the length and width of the segment are approximately equal; the lateral margins are almost parallel, the distal margin slightly rounded, and the inner distal surface gives rise to two spinelike processes.

The third thoracic leg of the third chalimus (Fig. 20*c*) is distinctly different from that of the second chalimus. It appears that the third chalimus marks a distinct change in the first three pairs of thoracic legs. The protopodite is now broader although the added breadth appears to have been gained as a result of a lengthening of the distal margin or an inclusion of the inner lateral margin with the distal; both the exopodite and the endopodite are now two-segmented and the armature has changed.

The protopodite of the third thoracic leg of the third chalimus is broad and flattened. The greatest width, across the proximal end, is slightly less than twice the length; the inner lateral margin appears to be incorporated into the distal margin although distinct evidence of this is lacking. A single plumose seta is present just lateral to the junction of the protopodite and sternal plate. The exopodite, attached to the lateral region of the distal protopodite surface, is two-segmented, the first segment slightly shorter than the second; the outer margin of the first segment is convex, the distal margin sloping to the proximal margin in older specimens but not distinctly so in younger specimens. The second segment is as wide as long, the lateral margins are irregular, the distal margin is rounded, and the surface bears three lightly plumose setae. The endopodite is two-segmented although the division between the first segment and the protopodite is indistinct in older specimens. The outer margin of the first segment is longer than the inner, and the proximal and distal margins are irregular. The second segment is approximately equal to the greatest length of the first segment and is almost circular in outline.

The protopodite of the third thoracic leg of the fourth chalimus (Fig. 20*d*) is broader than that of the third and the length has also increased so that the greatest proximal width is only about three-fourths of the greatest length.

TABLE 4

ARMATURE OF THIRD THORACIC LEGS OF DEVELOPMENTAL STAGES*

STAGE	MARGIN	STERNAL PLATE	PROTOPODITE	EXOPODITE 1	EXOPODITE 2	EXOPODITE 3	ENDOPODITE 1	ENDOPODITE 2
Chalimus I	outer		2p′	2h				
	inner			2h				
Chalimus II	outer			c,2h				
	inner			c			2h	
Chalimus III	outer		1p		3P			2P
	inner		1P,f				1P	1P
Chalimus IV	outer		1p		3P			1p,2P
	inner		1P,f				1P	1P
Chalimus V	outer		f,1P		c,4p′		c	c,2P
		f						
	inner		1P,f	1p,1H′	5P		1P	2P
Chalimus VI	outer		f,1P		c,1p′	c,3p′,1P	c	c,1p,3P
		f						
	inner		1P,f,2s	1H′	1P	3P	1P	2P
Adult	outer		f,1P		c,1p′	c,3p′,1P	c	c
		f						
	inner		1P,f,2s	1H′	c,1P	c,3P	1P	c,5P

* For explanation of symbols see Fig. 1.

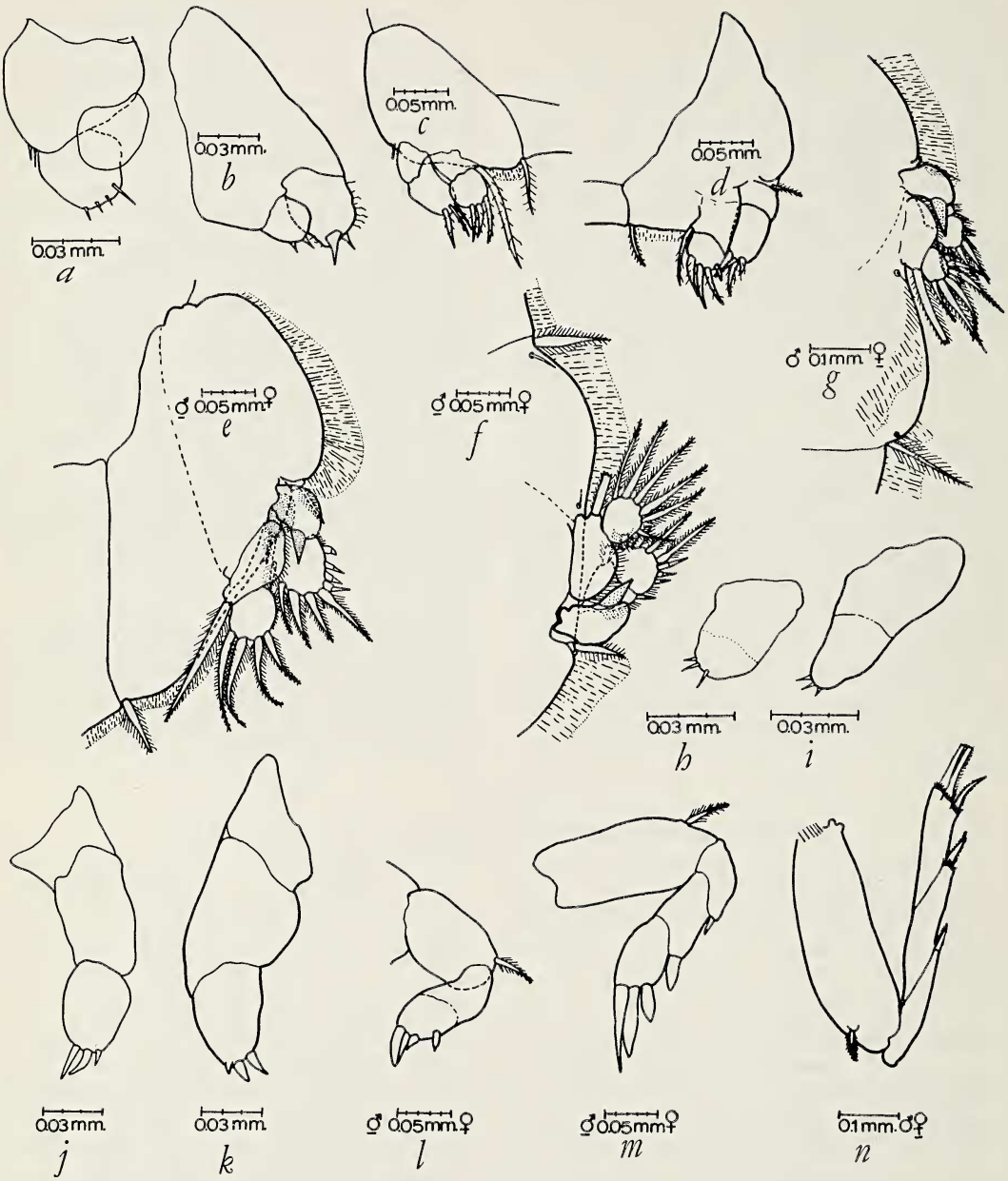

FIG. 20. Third and fourth thoracic legs of developmental stages of *L. dissimulatus*. *a–g*, Third thoracic legs: *a*, First chalimus; *b*, second chalimus; *c*, third chalimus; *d*, fourth chalimus; *e*, fifth chalimus; *f*, sixth chalimus; *g*, adult. *h–n*, Fourth thoracic legs: *h*, First chalimus; *i*, second chalimus; *j*, third chalimus; *k*, fourth chalimus; *l*, fifth chalimus; *m*, sixth chalimus; *n*, adult.

The protopodite tapers distally, the lateral margins are slightly irregular, and the distal margin is continuous with the outer lateral margin. The exopodite is two-segmented, the second segment 2½ times the length of the first. The base of the spine-bearing first segment of the fifth chalimus is visible inside the first segment of the fourth chalimus; the lateral margins of the fourth chalimus segment are convex. The spine-bearing segment mentioned above and present in the fifth and sixth chalimus in addition to the adult replaces the first segment of the third and fourth chalimus; the second segment of these two stages remains as the second segment, which later divides to form the second and third segments. The lateral and distal margins of the second exopodite segment of the fourth chalimus are continuous, the distal end is broadly rounded, and the surface gives rise to three lightly plumose setae. The endopodite is two-segmented although the division between the first segment and protopodite is indistinct and incomplete. The second segment is as wide as long and has a broadly rounded outline with the lateral and distal margins being continuous. The distal surface of the segment bears four lightly plumose setae.

The third thoracic leg of the fifth chalimus stage (Fig. 20*e*) possesses characteristics very similar to those of the adult. The protopodite is one-segmented and greatly expanded from the previous stage. The sternal plate, connecting the protopodites of the two legs, is broad and forms a laminate projection from the posterior ventral surface of the cephalothorax. The exopodite is still two-segmented, the first segment possessing a strongly-developed, spinelike projection from the inner distal surface. The proximal end of the first segment is distinct from the protopodite ventrally although it is still fused dorsally to the protopodite and the distal end to the second segment. The first segment, other than the process, is short, the width being greater than the length. The second segment is broadly rounded, the lateral margins continuous with the distal. The proximal end of the segment is narrow and the segment appears palm-shaped; the greatest width is slightly more than two-thirds of the length. The endopodite is two-segmented; the first segment is twice as wide as long and appears as a narrow band with a swollen outer lateral region. The second segment is attached to the inner distal surface of the first and is broadly rounded, the lateral and distal margins being continuous. The greatest length of the second segment is slightly greater than that of the first; the width and length are, however, approximately equal.

With minor exceptions, the third thoracic leg of the sixth chalimus (Fig. 20*f*) and the adult (Fig. 20*g*) are the same. The protopodite of the sixth chalimus is broadly flattened and laminate; the lateral and distal margins are continuous. The exopodite is now three-segmented, the first segment forming the base for a strongly developed, spinelike process that projects from the distal inner margin as in the preceding stage. The lateral margins of the first segment are irregular, the outer being generally convex and the inner almost straight. The second segment is short and flared from the narrow proximal to broad, concave distal end. The third segment is also short, being approximately equal in length to the second, and the width is slightly greater than the length; the lateral margins of the segment are rounded and continuous with the rounded distal margin. The endopodite is two-segmented, the first segment broad, its width approximately 1½ times its length. The outer two-thirds of the distal margin of the first segment is convex, the inner one-third concave; the outer lateral margin is continuous with the distal margin, and the inner margin is irregular. The second segment is slightly shorter than the first segment and is attached to the concave inner distal surface of the first. Both of the lateral margins are continuous with the distal margin in the second segment.

The protopodite of the adult third thoracic leg (Fig. 20*g*) is broader than that of the sixth chalimus; the first endopodite segment is slightly longer, although not wider, and the armature of the appendage has changed slightly in the moult from the sixth chalimus to the adult. Other than these differences, the appendages of the two stages are the same.

Thoracic Leg IV

The armature and character of the membranes, spines, and setae comprising the armature are given in Table 5.

The uniramous fourth thoracic leg is first

present in the first chalimus (Fig. 20*h*). The appendage in this stage is a one-segmented lobe. The proximal end is broader than the rounded distal end, the lateral margins are wavy, and the distal surface bears three spinule-like processes.

The fourth thoracic leg of the second chalimus (Fig. 20*i*) is lobate and somewhat longer than the appendage of the preceding stage. An indistinct division is present in the middle of the appendage, dividing it into two segments. Whether it is right to call the proximal segment of the appendage the protopodite and the remaining segments the exopodite as this author has previously done with regard to adult caligids (Lewis, in press) was not determined. For the present, however, because of the lack of definite information on this problem, the terms "protopodite" and "exopodite" will not be used but the segments simply referred to by number, with the proximalmost segment being the first. The proximal end of the first segment of the fourth thoracic leg of the second chalimus is broad and angled so that the appendage projects posteriorly and laterally from its junction with the fourth pedigerous segment. The second segment bears three short, terminal, spinelike processes.

The fourth thoracic leg of the third chalimus (Fig. 20*j*) has lost its general lobate shape and is now three-segmented. The first segment is short, its greatest length approximately three-fourths of the width; the segment is tapered from the broad proximal to somewhat narrower distal end. The second segment is about twice the length of the first and almost twice as long as broad; the lateral margins are irregular although basically parallel, and the distal and proximal margins are both irregular. The third segment is greater than one-half the length of the second, the lateral margins are flatly convex, and the distal margin is rounded and continuous with the inner lateral margin. Three spinelike processes are present on the distal surface of the third segment.

The fourth thoracic leg of the fourth chalimus (Fig. 20*k*) is somewhat similar to the third chalimus appendage. The length and width of the entire appendage is slightly greater than that of the preceding stage, the first segment is comparatively shorter and wider, the second segment appears swollen, and the third segment is not as distinctly separated from the second.

The fourth thoracic leg of the fifth chalimus (Fig. 20*l*) is three-segmented. The first segment is ovoid, the lateral and distal margins broadly rounded and the outer distal lateral surface bearing a single plumose setule. The division between the second and third segments is indistinct in contrast to the distinct division present in the preceding stage. The combined lengths of the second and third segments is approximately equal to that of the first segment. One poorly developed spine is present on the outer distal lateral surface and two well-developed and one poorly developed spines are borne on the distal surface of the third segment.

The fourth thoracic leg of the sixth chalimus (Fig. 20 *m*) is four-segmented. The first segment is slightly longer than the combined lengths of the three distal segments, the proximal and distal ends of the segment are slightly narrower than the middle of the segment, and the lateral margins are wavy. A single plumose setule is present on the outer distal lateral surface of the segment, as in the preceding stage. The second segment is short, its greatest length slightly less than that of the third segment; the lateral margins are flatly convex, the outer much longer than the inner. A short, simple spine is present on the outer distal corner of the second segment. The third segment is tapered from the proximal to slightly broader distal end; the lateral margins are flat or flatly convex, the outer longer than the inner. A single simple spine is present on the outer distal corner of the segment. The fourth segment is slightly broader

TABLE 5

ARMATURE OF FOURTH THORACIC LEGS OF DEVELOPMENTAL STAGES*

STAGE	MARGIN	SEGMENTS 1	2	3	4
Chalimus I	outer	3h			
Chalimus II	outer		3h		
Chalimus III	outer			1h,2H	
Chalimus IV	outer			1h,2H	
Chalimus V	outer	1p		1h,1h,2H	
Chalimus VI	outer	1p	1h	1H	3H
Adult	outer	1p	1H	1H	3H

* For explanation of symbols see Fig. 1.

TABLE 6

MEAN LENGTH OF ATTACHMENT FILAMENT

	COPEPODITE	CHALIMUS 1	2	3	4	5	6
Measurement (in mm)	0.136	0.111	0.146	0.156	0.155	0.163	0.213
Number of specimens	1	6	30	13	60	7	2

distally than proximally; the lateral margins are flatly convex, the distal surface almost flat and bearing three simple although well-developed spines. The innermost of the three terminal spines is longest, the outermost shortest.

The make-up of the fourth thoracic leg of the sixth chalimus is similar to that of the adult (Fig. 20*n*) although the armature is more simple. The segments of the adult, particularly the distal three, are more elongate; the terminal spines on each segment have at least one denticulated or frilled margin and are encircled by a frilled process at their base.

Caudal Rami

The caudal rami are first present in the copepodite stage (Fig. 12*a*). These structures, in the copepodite, are slightly more than one-half of the greatest length of the combined genital segment and abdomen and their greatest width is approximately equal to the length. Both of the lateral and the distal margins are irregular. Two short, plumose setae are present on the proximal one-half of the outer lateral surface and two long, plumose setae arise from the distal surface.

The caudal rami of the first chalimus (Fig. 12*b*) arise from the posterior ventral surface of the genital-abdominal segment. The greatest length of the rami is approximately two-thirds of the width; the lateral and distal margins are continuous. Six plumose setae are present on the rami, two on the distal lateral surface, three on the distal surface, and one on the inner distal corner.

The caudal rami of the remaining chalimus stages and the adult (Fig. 12*c–l*) are similar in shape and make-up to the rami of the first chalimus. Minor differences such as the setulation of the inner margin in the second chalimus (Fig. 12*c*) and succeeding stages and a variation in the length of the setae are the only significant changes that occur after the first chalimus.

REMARKS ON BEHAVIOR OF DEVELOPMENTAL STAGES AND THEIR RELATION TO HOST

Both of the planktonic first and second naupliar stages exhibit a strongly positive phototropism in the laboratory. Movement in both of these stages is sporadic and jerky, the three pairs of appendages present on each of these stages moving in unison in a series of strokes and then remaining motionless for a short period of time. The animal thus makes a short but swift movement and then rests, sinking gradually. Whether it is the response to light or a more intrinsic factor that controls the amount of time spent in swimming and in resting was not determined. The function of the balancers present on the posterior end of the nauplii has been suggested to be the balancing of the nauplius when it is at rest (Wilson, 1905:538). Since these structures were not seen to move to any extent in *L. dissimulatus,* their function cannot be definitely ascertained although their structure and position do suggest that they play a role in the positioning of the nauplius during both movement and rest.

As the age of the second nauplius increases, the positive reaction to light decreases, a condition that extends into the planktonic phase of the copepodite. A light placed on one side of a finger bowl caused some copepodites to swim towards that side. The tendency, however, was not as great as in the naupliar stages and appeared to diminish as the age of the copepodites increased. The movement of the copepodite was quite rapid although jerky and irregular; the periods of time spent in swimming were longer, and the time spent in resting shorter than in either of the two naupliar stages. During the resting phase the copepodite appeared to sink

faster than did the nauplius, which can be explained by the apparent increase in body volume and the decrease in relative number and length of setae. Copepodites were kept up to 72 hours in culture. After about 10 hr they began to prod the bottom and sides of the dish with the anterior end of their body. Inasmuch as the copepodite is the attachment stage, the prodding may have some relation to the attachment of the animal to its host.

As was mentioned earlier, attachment was observed in only one copepodite. Attachment was accomplished by hooking the strong, claw-like terminal processes of each second antenna into the substrate. The formation of the attachment filament was not seen in the single copepodite that attached in the laboratory. To determine the means by which the filament was formed, several copepodites were collected that had attached to the host and formed a filament. These animals were separated from the host by severing the filament close to the body of the copepodite. A piece of loosely woven nylon cloth was then placed in a finger bowl and the detached copepodites placed in with it. Those specimens that reattached did so by holding themselves to the cloth substrate by means of their maxillipeds and second antennae. They then placed their body at an angle to the substrate, with the anterior end in close proximity to it, and, by jabbing the substrate with the middle of the frontal region, they appeared to secure either the remaining attachment filament or a new filament formed by a secretion that hardened almost immediately on the substrate as an irregular lobe, not the disk found in copepodite and chalimus specimens normally attached to the host. After the filament was attached, the terminal processes of the maxillae were used to stroke the filament between the frontal region and the substrate while the copepodite backed off from the point of attachment. The backing off of the animal appeared to cause the materal secreted by the frontal organ, either before or after the animal started backing off, to be drawn out into a filament and the stroking by the maxillae to make the filament more even.

After the attachment, the activity of the copepodite decreased. This observed lower activity rate was noted for the first four chalimus stages although activity did increase to some extent during the actual shedding of the old cuticle in moulting.

Heegaard (1947:90–94) indicates that the various attached stages of *Caligus curtus* secrete the attachment filament anew each time a moult occurs. During the period of moulting observed in both copepodite and chalimus stages in *L. dissimulatus,* the original filament remained attached to the animal, the cuticle rupturing on the anterior dorsal surface and the animal, by vigorous movements of its body, freeing itself from the old cuticle and passing it posteriorly over the posterior end of the body. The shed cuticle did not remain attached to the host or to the frontal filament. Heegaard (1947: fig. 32) figures a portion of the fin ray of a cod with several attachment filaments of *Caligus curtus* hanging from it and (1947:92) suggests that these are left by the various chalimus stages. The only attachment filaments that were observed in host tissue and could be definitely tied in with a chalimus were those from specimens of the fifth and sixth chalimus stages of *L. dissimulatus* that had just broken free and assumed the free-moving adult type of existence.

Gurney (1934:184, 186, 188) indicates that the attachment filament is increased in length slightly at each moult as indicated by the small annuli at the proximal end of the attachment filament of later chalimus larvae. This could not be verified or disproved for *L. dissimulatus,* as the attachment filament is irregular at the proximal end at all stages of development, from the copepodite to specimens of the sixth chalimus that are still attached. The mean length of the filament during each stage is given below in Table 6 and suggests that a small amount of new material is added although the lack of specimens in some of the stages does not provide substantial proof of this.

Shiino (1959:305) reports chalimus larvae and young stages of *L. dissimulatus* from the gills of *Bodianus diplotaenia* captured in the Revilla Gigedos Islands and includes several figures of these stages. This report is of interest because of the place of attachment of the chalimus larvae. With only two exceptions, all of the chalimus larvae of Hawaiian specimens of *L. dissimulatus* were found attached to the upper surface of the buccal cavity of the host. The

two exceptions were chalimus larvae found attached to the gill membrane of *Acanthurus triostegus sandvicensis*. The number of larvae present in the buccal cavity of infected fishes ranged from 1 to 203. In the specimen of *Acanthurus olivaceus* possessing 203 attached copepodites and chalimus larvae, the roof of the mouth appeared to be actually shingled with copepods.

After breaking free from the attachment filament, the fifth or sixth chalimus moves out of the buccal cavity either into the gill cavity or onto the external surface. The final moult, from the sixth chalimus to the adult, is accomplished outside of the buccal cavity. Only one observation of the final moult was made and this was after the adult had broken through a split in the anterior dorsal surface of the sixth chalimus cuticle. At the beginning of the observation the animal had pulled the second antennae free from the old cuticle and was not actively moving, holding on to the host by means of the maxillipeds and keeping the second antennae free. After a short period of time the second antennae were used to grasp the surface and the maxillipeds and remaining appendages were pulled free from the cuticle. By means of violent wriggling of the body and appendages, the cuticle was shed over the posterior end of the body. After a second short period of time, during which the newly emerged adult remained attached by the second antennae, all of the thoracic appendages and the maxillae were moved randomly and the animal then assumed the adult role of skittering over the surface of the host.

Fertilization occurs just after the terminal moult. The male at this stage of development is almost completely grown; the female is still small and will increase in size in the adult stage. The actual placement of the spermatophores, held within the genital segment of the male, was not observed. Several mating pairs were collected and observed, however. The male was found to clasp the fourth pedigerous segment or the anterior end of the genital segment of the female with the second antennae. The function of the maxillipeds in mating was not determined, although in all observed pairs the maxillipeds of the male were free. A. Scott (1901:28) and Wilson (1905:528) indicate that the caligid spermatophore is viscid and, as noted for *L. dissimulatus,* that it forms an oval or tear-shaped body in the posterior region of the genital segment. The male presumably bends the posterior region of its body, the free segments, underneath itself and, upon contact with the posterior ventral surface of the female, discharges the two spermatophores which adhere to the genital segment of the female. No remating was observed and, as suggested by Wilson (1905:527), the single mating just after both sexes moult into the adult probably suffices for the entire egg production of the female.

The young adult female was found in both the gill cavities and on the external surface of the body. Large females carrying egg strings were found primarily in the gill cavity. The copepod appears to have more protection in the gill cavity, especially against being swept off of the host by water currents or brushed off when the host comes in contact with the substrate. The position of the female on the host thus may be dependant upon its size and upon the presence or absence of egg strings which, it appears, add a considerable burden.

The duration of the adult life is not known. Females kept in the laboratory produced up to three sets of egg strings, each string being extruded approximately 21 hr after the previous string had hatched. Thirty to 40 hr is the average interval between extrusion of the eggs and hatching. The period of time between fertilization and the production of the first pair of egg strings is not known, neither is the time from moulting into the adult until the female is fertilized. Further, the conditions provided in the laboratory were far from those in the natural environment and it is felt that the number of egg string sets produced is probably more than the three obtained in the laboratory.

SUMMARY

1. The external anatomy of the 10 stages in the life history of *Lepeophtheirus dissimulatus* is described and figured.

2. The general behavior of the various stages is discussed. The first two, the naupliar stages, are planktonic. The third or copepodite stage is planktonic early in its existence but later attaches to the fish host by means of the prehensile second antennae. After attachment, the copepodite secretes a frontal filament that is em-

bedded in the tissue of the host and enables the copepodite and following attached larval stages to remain attached to the host without using their appendages. At least four of the six chalimus stages that follow the copepodite remain attached to the host by the frontal filament; the fifth and sixth chalimus stages may either be found attached or free on the host. The adult is found moving freely over the surface of the host.

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